#6

#6

Fisheries Research Bulletin No. 6

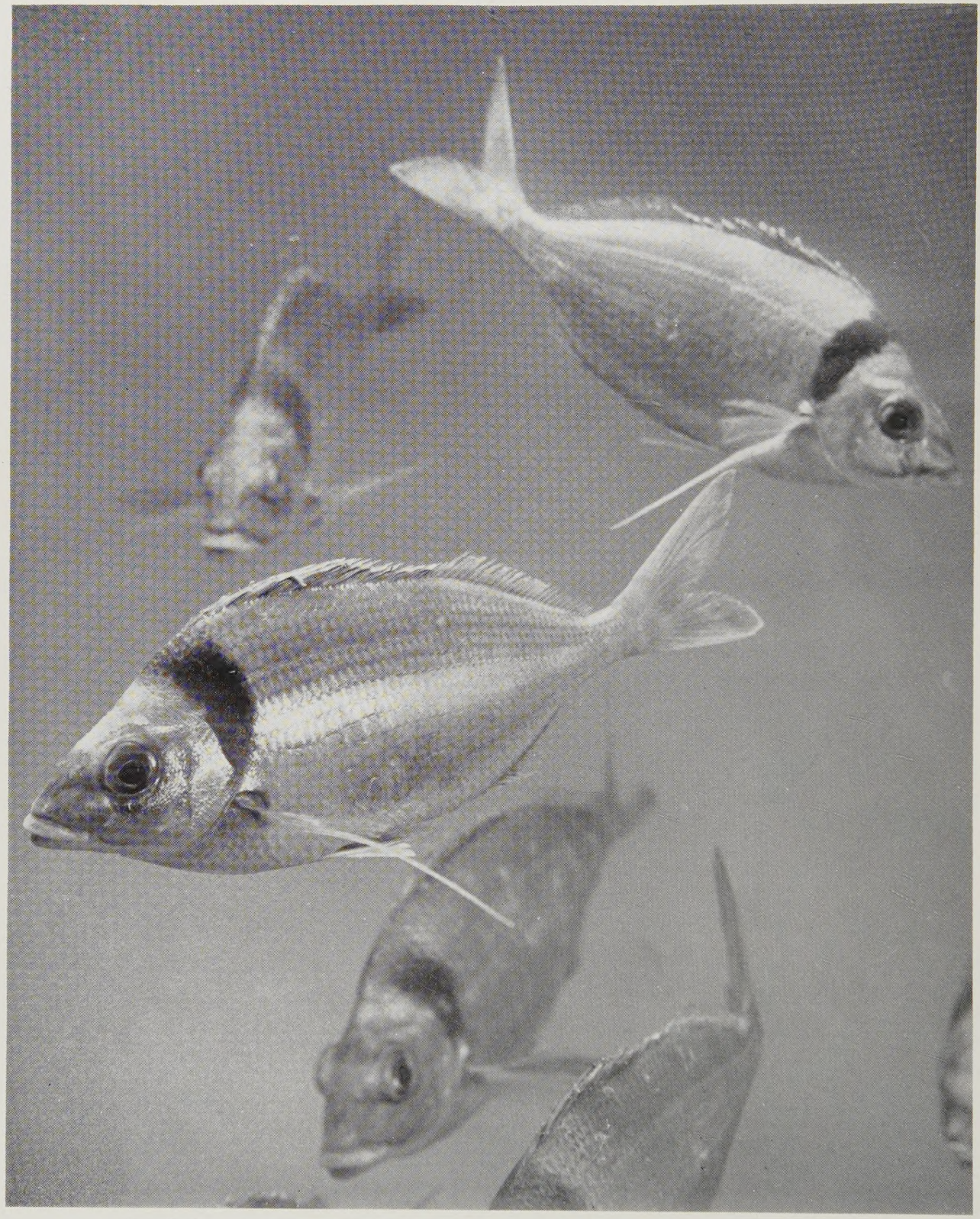
The Biology of the New Zealand Tarakihi, *Cheilodactylus macropterus* (Bloch and Schneider)

LIBRARY
FEB 1 5 1973
FISH & WILDLIFE SERVICE

By
L. J. Tong and C. M. Vooren

Fisheries Research Division
New Zealand Ministry of Agriculture and Fisheries

The Biology of the New Zealand Tarakihi, *Cheilodactylus macropterus* (Bloch and Schneider)



Frontispiece: A group of tarakihi in the aquarium at the Fisheries Research Division.

Fisheries Research Bulletin No. 6

The Biology of the New Zealand Tarakihi, *Cheilodactylus macropterus* (Bloch and Schneider)

By

L. J. Tong and C. M. Vooren,

Fisheries Research Division, Ministry of Agriculture and Fisheries, Wellington, New Zealand

Fisheries Research Division

New Zealand Ministry of Agriculture and Fisheries

Published by the New Zealand Ministry of Agriculture and Fisheries
Wellington
1972

This series of research bulletins, which was begun in 1968, was formerly published by the New Zealand Marine Department before the Fisheries Research Division was transferred from that Department to the Ministry of Agriculture and Fisheries in September 1972.

FOREWORD

FOR MANY YEARS the tarakihi has been the second most valuable commercial fish species in New Zealand. It was therefore important that as much basic biological information as possible should be available as a background to work on the commercial fishery. The combined and complementary studies of Dr Tong and Mr Vooren have been designed to provide such information, and this publication is a measure of the effectiveness of their collaboration.

Although publication was originally planned as a series of separate papers, it seemed more appropriate to publish this preliminary work of theirs in a single bulletin. In this way the information is readily and conveniently accessible to fisheries biologists and industry alike.

G. DUNCAN WAUGH,
Director, Fisheries Research Division.

Digitized by the Internet Archive
in 2025

https://archive.org/details/new-zealand-fisheries-research-bulletin_1972_6

CONTENTS

		Page
CHAPTER 1: INTRODUCTION		11
CHAPTER 2: AGE DETERMINATION	*C. M. Vooren and L. J. Tong*	13
Introduction		13
Material and Sampling Techniques		13
Description of the Otolith		13
Analysis of Otolith Zonation		16
Ageing		20
Zone Formation and Age		24
Zone Formation in Different Sea Areas		24
Comparison of Otolith Readings		25
Discussion		26
CHAPTER 3: AGE AND GROWTH	*C. M. Vooren*	28
Material and Methods		28
Age Composition		28
Seasonal Growth		28
Annual Growth		29
Length-weight Relationships		33
CHAPTER 4: BREEDING BIOLOGY	*L. J. Tong*	35
Introduction		35
Material and Methods		35
Results		35
Discussion		44
CHAPTER 5: GAMETOGENESIS	*L. J. Tong*	46
Introduction		46
Material and Methods		46
Observations		46
Results		50
Spermatogenesis		51
Correlation of Microscopic Changes with the Maturity Stage Index		53
Discussion		53
SUMMARY		56
ACKNOWLEDGMENTS		56
REFERENCES		57

FIGURES

Page

1. The localities where fish samples were taken between 1967 and 1970 14
2. A tarakihi otolith 15
3. Otoliths of tarakihi of different ages shown at the same magnification 16
4. A tarakihi otolith, showing checks and double rings 17
5. Marginal increment width-frequency distributions of the combined Bay of Plenty samples 18
6. Marginal increment width-frequency distributions of the sexes within ring groups 20
7. Length-frequency distributions of a series of samples from a single station in Tasman Bay 21
8. Length-frequency distributions of total samples and of ring groups, plotted as percentages of the total sample 22
9. Results of age determination of a spring sample 23
10. Length-frequency distributions of age groups, as determined from rings and m.i. widths, plotted as a percentage of the total sample 24
11. Monthly mean width of "recent layer" on the otoliths of age groups 3 to 7 25
12. Comparison of repeated otolith readings by two observers 27
13. Age composition and fish density 29
14. Monthly mean length of age groups 4 to 9 30
15. Growth curves of tarakihi in the Bay of Plenty and the East Cape area 32
16. Ford-Walford regression for age groups 1 to 14 33
17. Monthly mean weights of fish of 30, 35, and 40 cm 33
18. Length-frequency distributions of males and females in the Bay of Plenty 36
19. Age-frequency distributions of males and females taken between March and June 1969 37
20. Average length of each age group for the period March to June 1969 38
21. Gonad weight shown as a percentage of gutted body weight 39
22. Analysis of maturity stage frequency for the period February to July 1968 40
23. Analysis of maturity stage frequency for the period March to June 1969 41
24. Analysis of maturity stage frequency for the three areas sampled in January-February 1968 42
25. Sex ratio of each length group 43
26. Transverse section of a resting ovary, showing lamellae and primary oocytes 47
27. Transverse section of an ovary, showing a nest of developing oogonia 47
28. Fully developed primary oocyte 48
29. Transverse section of a mature ovary, showing various stages in egg development 48
30. Detail of egg 49
31. Evacuated follicles 49
32. Transverse section of an ovary, showing numerous resorbing eggs 50
33. Transverse section of an ovary of a returned tagged fish, showing late stages in resorption and normal development 50
34. Transverse section of a testis, showing early stage in spermatogenesis 51
35. Transverse section of a testis, showing the various stages in sperm formation 52
36. Transverse section of a mature testis, showing lobules filled with sperm 52
37. Transverse section of a semi-spent testis 53

TABLES

Page

1. Percentages of tarakihi showing narrow m.i. in samples from three stations in the Bay of Plenty 25
2. Comparison of otolith readings by two readers 26
3. Estimates of age composition and mean length per age, based on independent readings of sample 5 by two readers 26
4. List of sampling dates 28
5. Analysis of variance of length of age groups 5 to 7, between sampling stations and between sexes, for individual months 30
6. Analysis of variance of length of age groups 5 to 9, between sampling stations and between sexes, for the combined samples of March, April, May, and July 1969 31
7. Analysis of variance of length of males and females of age groups 6 to 8, between sampling stations, and percentage of females at the stations for the combined samples of March, April, May, and July 1969 31
8. Mean lengths of the age groups from the samples collected in March to July 1969 31
9. Mean weights of the age groups from the samples collected in March to July 1969 32
10. Estimates of t_0 33
11. Relationship between body weight and body length 34
12. Maturity stages for male tarakihi 36
13. Maturity stages for female tarakihi 36
14. Average lengths of each maturity stage for February to April 1968 38
15. Average length of each maturity stage for March and April 1969 39
16. Percentage mature at each age group 42
17. Percentage mature at each length group 43
18. Sex ratio of the catches, Bay of Plenty, 1967–69 44
19. Summary of available data on the spawning period of *C. macropterus* 45
20. Average percentage frequency of the various stages in oogenesis over an 11-month cycle 51
21. Average percentage frequency of the various stages in oogenesis for each stage in the maturation cycle 51
22. Histological description of each maturity stage in males 53
23. Histological description of each maturity stage in females 53

CHAPTER 1

INTRODUCTION

The tarakihi, *Cheilodactylus macropterus* (Bloch and Schneider), is the second most important species of wet fish landed in New Zealand. Tarakihi stocks are exploited by trawling, and to a small extent by Danish seining and long lining, from the Three Kings Islands in the north to Stewart Island in the south and also in the Chatham Islands. They are normally caught at depths ranging from 10 to 200 m, the greatest catches usually being taken in waters deeper than 100 m (Tong and Elder 1968).

Despite the economic importance of tarakihi, little is known of the biology of the species in New Zealand or elsewhere in its range. Much of the published material is brief and provides scant biological information, and some of the publications are in the form of reports which do not deal fully with the work they describe. The notes on *C. macropterus* at the Indian Ocean islands of Amsterdam and St. Paul by Angot (1951) include a description and discuss distribution, length frequency of catches, ageing from scales, food and feeding habits, and observations on the spawning behaviour. McKenzie (1961) gave a short account of the work she carried out on the New Zealand tarakihi, including life history, growth, food and feeding, migrations, abundance, and general ecology, and Han's (1964) report contains brief information on the spawning season, age and length at first maturity, growth rate, food, and catch per effort of the species in New South Wales waters. Other brief notes are those of Graham (1939) on the spawning of tarakihi off Otago and of Phillipps (1926) on diet.

To provide a better understanding of the biology of the tarakihi in New Zealand, a more detailed study was begun in 1967 in the Bay of Plenty. The results of this work are presented in this bulletin.

The tarakihi is a percoid belonging to the family Cheilodactylidae. It was first described by Bloch and Schneider (1801) under the name of *Cichla macroptera* from specimens caught during one of Captain Cook's voyages to New Zealand. The fish was given the Maori name tarakihi. Later Cuvier and Valenciennes (1830) placed the tarakihi in the genus *Cheilodactylus*, which had been established by Lacépède (1803), but at the same time they replaced the specific name *macropterus* with *carponemus* without giving reasons. Whitley (1957) lists these and all other synonyms, using *Nemadactylus macropterus* as the valid name. The genus *Nemadactylus* was described in 1839 by Richardson and was based on a post-larval specimen caught off Tasmania, and Whitley (1957) appears to have accepted Richardson's reasons for setting up the new genus.

We are unable to comment on the validity of Whitley's action and hence in this account we retain the name most frequently used and refer to the species as *Cheilodactylus macropterus* or tarakihi.

There are several descriptions of *C. macropterus* (Bloch and Schneider 1801, Richardson 1839, Waite 1911, Ribeiro 1915, Devincenzi 1924, Angot 1951), but for New Zealand waters we refer to Waite's (1911) account.

The most characteristic features of the tarakihi are the elongated pectoral ray and the black band extending from the anterior margin of the dorsal fin almost to the base of the pectoral fin (see frontispiece). Fin ray counts as taken from Waite are B. vi.; D. xviii. 28; A. iii. 15; V. i. 5; P. 9 + 6; C. 16 + 6. The body is oval and laterally compressed, reaching its greatest depth at about the level of the seventh spine of the dorsal fin. The head is small and about one-quarter of the length to caudal fork. The small mouth is protractile, with thick lips. The body colouring is silvery grey ventrally and brownish above the lateral line. No sexual dimorphism has been observed.

Another representative of the genus, the porae (*C. douglasii* (Hector)) occurs in New Zealand waters, but it is far less abundant than the tarakihi. The porae is distinguished from the tarakihi by the absence of the black nuchal band and by the numbers of dorsal (xvii–xix, 26–30), anal (iii, 16–17), and pectoral (8–9 + 6–7) fin rays (Whitley 1957).

The widespread distribution of tarakihi in New Zealand and its economic potential were not recognised until the Government trawling expedition of 1907, when Waite (1911) stated in his report:

"Of all the fishes taken, economic or otherwise, this was the most ubiquitous species secured". In Australian waters *C. macropterus* is found off New South Wales, Victoria, and Tasmania, in the Great Australian Bight, and off southern Western Australia (Roughley 1951). Berg (1895), Ribeiro (1915), and Devincenzi (1924) have all reported the occurrence of the species from Mar del Plata, Brazil, and more recently Angot (1951) published descriptions and habits of the "poisson bleu", *Chilodactylus macropterus*, from Amsterdam and St. Paul Islands in the Indian Ocean.

CHAPTER 2

AGE DETERMINATION

By C. M. Vooren and L. J. Tong

INTRODUCTION

The otoliths of many fish species consist of alternating concentric layers of opaque and hyaline material. Studies on otolith structure for age determination have always been made on the saccular otolith (sagitta), as this is by far the largest of the three otoliths in the teleost labyrinth and shows the concentric stratification most clearly. In many species the formation of opaque and hyaline layers is an annual or seasonal phenomenon, and the otolith structure then gives an indication of the age of individual fish (Graham 1929, Hickling 1933, Gambell and Messtorff 1964). Such a pattern of opaque and hyaline zones is found in the otolith of the tarakihi, *Cheilodactylus macropterus*. The aim of the present study was to determine whether the zonation of the otoliths of this species is sufficiently clear and regular for zones to be counted in a uniform, well-defined manner, and, if so, to ascertain the time intervals that are represented by these zones.

MATERIAL AND SAMPLING TECHNIQUES

Sampling Plan

Samples of adult and sub-adult fish were collected in the Bay of Plenty at regular intervals during 1968-69 at the following stations (Fig. 1):

Slipper Island 37° 04′ S, 175° 58′ E, depth 45 to 50 m.

Motiti Island 37° 38′ S, 176° 30′ E, depth 60 to 70 m.

Plate Island 37° 33′ S, 176° 33′ E, depth 150 to 200 m.

Small juvenile fish were not found in significant numbers in the Bay of Plenty, but samples of this category were collected during 1969-70 in the following localities (Fig. 1):

Tasman Bay (series) 40° 55′ S, 173° 16′ E, depth 40 m.

Tasman Bay (1 sample) 40° 44′ S, 173° 42′ E, depth 50 m.

Golden Bay 40° 37′ S, 172° 54′ E, depth 24 m.

North Otago 45° 16′ S, 171° 16′ E, depth 65 to 70 m.

Hawke Bay 39° 05′ S, 177° 03′ E, depth 16 to 20 m.

The fish were caught by bottom trawl with 11.5-cm stretched cod-end mesh and 2.5- or 3.8-cm stretched cod-end liner mesh. Otoliths were collected from random samples of fish, either the whole catch being taken or a simple random subsample of 100 fish drawn from the catch. Some of the juvenile samples are stratified random samples with proportional allocation, 1-cm length groups being used. The fork length of the fish was measured to the nearest centimetre below the actual length.

Removal and Storage of Otoliths

Each otolith lies in the cranium of the fish, and in lateral view its position is behind the eye and exactly underneath the posterior edge of the preopercular bone. Externally this edge of the preopercular is visible as a vertical groove. If the cranium is split open from the dorsal side with a heavy-bladed knife so that the cut runs just in front of the vertical groove, the otoliths can be removed from the saccular cavities with forceps. They can then be wiped clean and placed in envelopes.

The contrast between hyaline and opaque zones is much sharper in otoliths that have been dried than in otoliths that are fresh or have been kept in watery solutions. We therefore stored the otoliths dry in black plastic trays fitted with lids and with 25 compartments for individual pairs of otoliths. When stored in this manner otoliths are easily examined, the collections can be filed conveniently, and the otoliths are not easily damaged.

DESCRIPTION OF THE OTOLITH

The tarakihi otolith is oblong and shaped like a curved plane, the convex surface facing the brain and the concave surface facing outward. A diagram of the otolith viewed from the concave side is

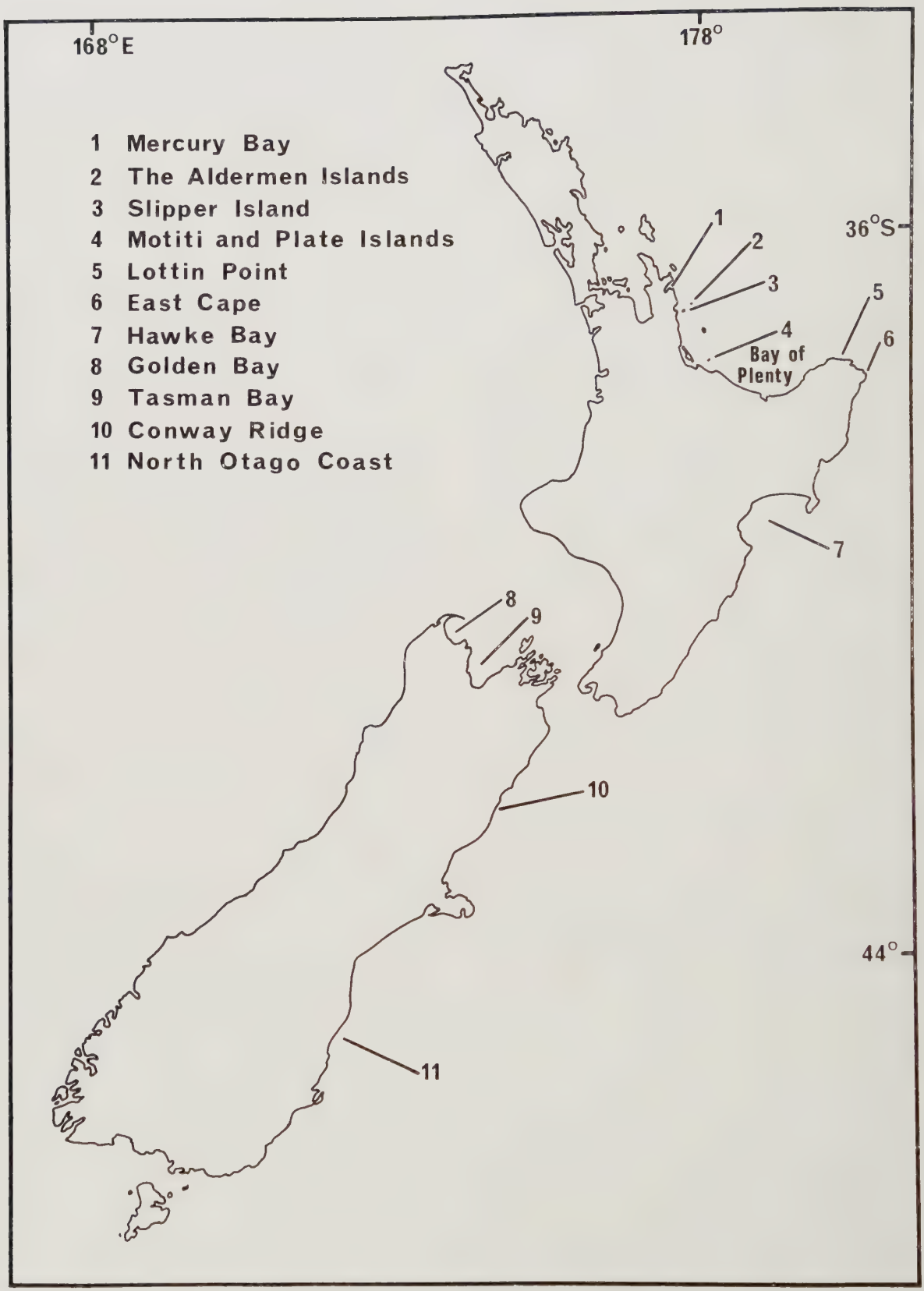


Fig. 1: The localities where fish samples were taken between 1967 and 1970.

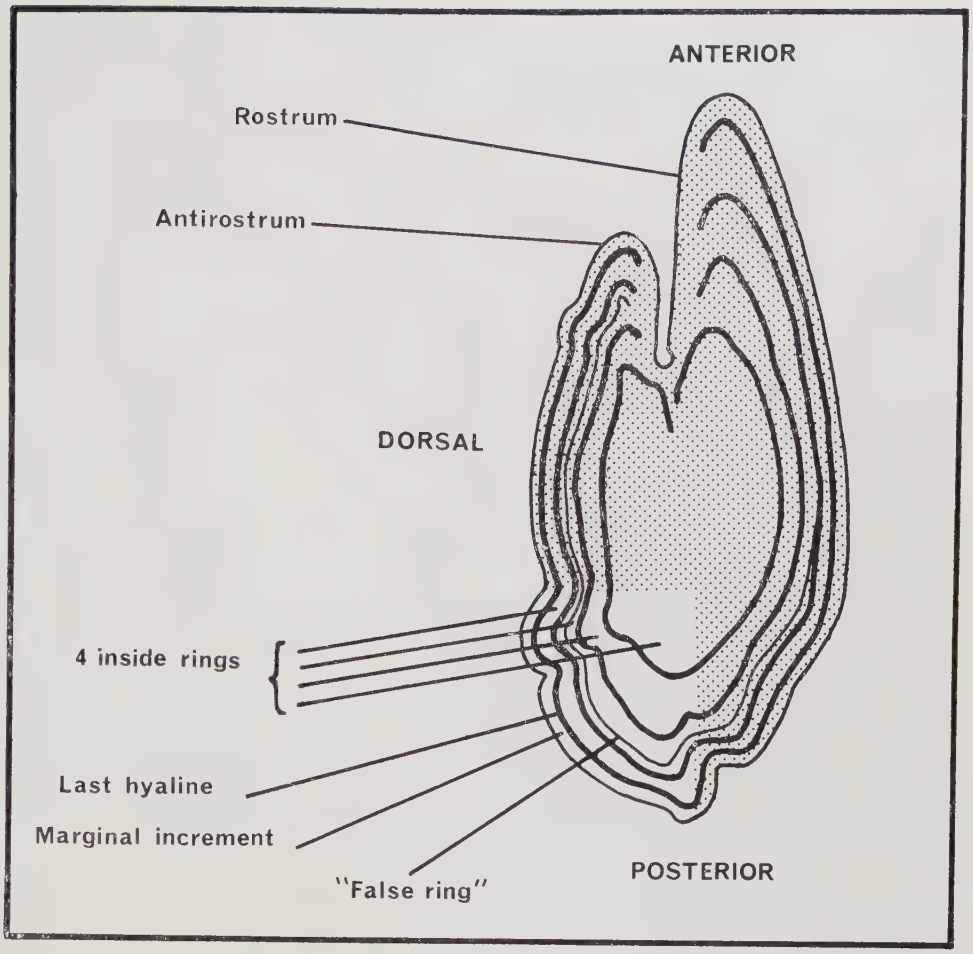


Fig. 2: A tarakihi otolith. Hyaline zones are indicated by heavy black lines. The unshaded part of the otolith is the dorso-posterior area in which the measurements were made.

shown in Fig. 2; Figs. 3 and 4 show otoliths viewed from this same side. Typical features are the pronounced rostrum and antirostrum and the indentation of the dorsal edge. The rostrum and antirostrum often break off and are lost during the collection of otoliths. The indentation of the dorsal edge becomes larger and more irregular in older fish. In the small otoliths of juvenile fish the rostrum is less pronounced and the dorsal edge is relatively smooth (compare Figs. 3a and 3c). The otoliths of the larger fish (35 to 45 cm) are 7 to 10 mm in total length and weigh 25 to 30 mg.

The otoliths, wholly immersed in cedarwood oil, were examined with reflected light under a low-power binocular microscope against a dark background. Under these conditions opaque zones appear white and hyaline zones grey or black (Figs. 3 and 4). Fine details show up more clearly in cedarwood oil than in xylene, dilute glycerine, or water.

The terminology used in the following description is taken from Jensen (1965). Unless specified otherwise, counts of otolith zones in this section and following sections will refer to the number of opaque zones, counted from the centre outward and including the nucleus. The width of an opaque zone is the distance between two consecutive hyaline zones.

Nucleus

The otoliths from all sampling areas show an opaque nucleus containing a hyaline central area. The latter has no clear outline; there is a gradual transition from hyaline to opaque. The hyaline centre is clear in otoliths of small fish, but less evident in the thicker otoliths of larger fish (compare Figs. 3a and 3c).

Zones

The concave side of the otoliths shows a clear pattern of alternating wide opaque and narrow hyaline zones or "rings". The zonation is blurred on the rostrum and the ventral side, but well defined on the dorsal and posterior sides. The outline of the first hyaline zone is clear in the small otoliths of young fish, but is obscure in some larger otoliths (compare Figs. 3a, 3b, and 3c). Normally the opaque zones decrease gradually in width and opacity from the centre outward until a minimum

Fig. 3: Otoliths of tarakihi of different ages shown at the same magnification. a: North Otago, November 1969; ring group 2, narrow m.i., so age group 2; fish length 19 cm. b: North Otago, November 1969; ring group 4, wide m.i., so age group 5; fish length 31 cm. c: Motiti Island, December 1968; ring group 15, narrow m.i., so age group 15; fish length 40 cm.

width is reached in the eighth or ninth zone, after which the zones are the same width, though they may become less opaque (Fig. 3c). In some otoliths the change is not gradual and after the fourth to sixth zones the width and opacity of the other zones lessen abruptly.

Checks

Checks are hyaline marks that do not fit in with the overall zonation pattern and are therefore ignored when zones are counted. These hyaline marks are indistinct, narrow, and irregularly spaced in comparison with the "true" hyaline zones in the same otolith; some do not run completely round the otolith or are much interrupted (Figs. 2 and 4). A check can occur in the middle of each of a series of opaque zones, which produces a pattern of "double rings". This type of check has been observed only in the narrower zones after the third (Fig. 4).

To distinguish checks from true zones the overall pattern of the otolith has to be looked at under low magnification. Hickling (1933) noted the same for the otolith of the hake, *Merluccius merluccius* (L.).

Edges

Some otoliths show edges that are obviously either opaque or hyaline (for example, Fig. 3a). Usually, however, the margin is more transparent than the material just inside it, irrespective of month or season, and no distinction between hyaline or opaque edges can be made.

ANALYSIS OF OTOLITH ZONATION

To determine the relationship between otolith structure and age of fish, two methods were followed:

(a) Analysis of the annual record of marginal growth. This method consists of examining the edge of otoliths collected at regular intervals during a year from one particular area; in this way the periodicity of the zone formation can be determined.

(b) Comparison between zone counts and Petersen's method. The latter method is a

technique of recognising age groups in populations by analysis of polymodal length-frequency distributions. Graham (1929) and Hickling (1933) describe how this method can be applied and how the otolith structure can be related to the known age of the fish.

In this bulletin the seasons have been defined as follows:

Spring: September to November.

Summer: December to February.

Autumn: March to May.

Winter: June to August.

The Annual Record of Marginal Growth

As the nature of the edge of tarakihi otoliths is hard to determine, we could not use the qualitative method of classifying the otoliths by eye into those with opaque and those with hyaline edges, as has been done for many other species (Hickling 1933, Irie 1957, Gambell and Messtorff 1964). We have therefore chosen a quantitative method similar to the one used on fish scales by Hanabuchi (1967), Kojima (1967), Murakami and Okada (1967), and Cragg-Hine and Jones (1969). In the dorso-posterior quarter of the otolith, where the zone pattern is most clear and regular, a measurement was made of the width of the area situated outside the "last hyaline" zone, the latter being the outermost hyaline zone with opaque material on both sides. This area outside the "last hyaline" is the "marginal increment", abbreviated as m.i. (Fig. 2). The m.i. consists of an opaque zone with or without a hyaline margin, and it follows from the definition that the m.i. width can never be zero. The width of the m.i. was measured from its inside edge outward, with a binocular microscope with eyepiece micrometer, at magnification x 40. All measurements were made and recorded in micrometer units, and values were rounded off to the nearest whole number of units. At the magnification used 1 micrometer unit was equivalent to 0.024 mm. The number of "inside rings", that is, the number of opaque zones inside the "last hyaline", was recorded with each m.i. measurement. The specimens with the same number of inside rings are referred to as a "ring group".

Measurements were made on a series of 22 samples collected in the Bay of Plenty between November 1968 and December 1969. The ring groups 4, 5, and 6 were sufficiently abundant in all samples to provide a complete record of the change of m.i. width with time; most samples contained 20 or more specimens of each ring group. Figure 5 shows the percentage frequency distributions of m.i. width by ring group and month. The distributions were

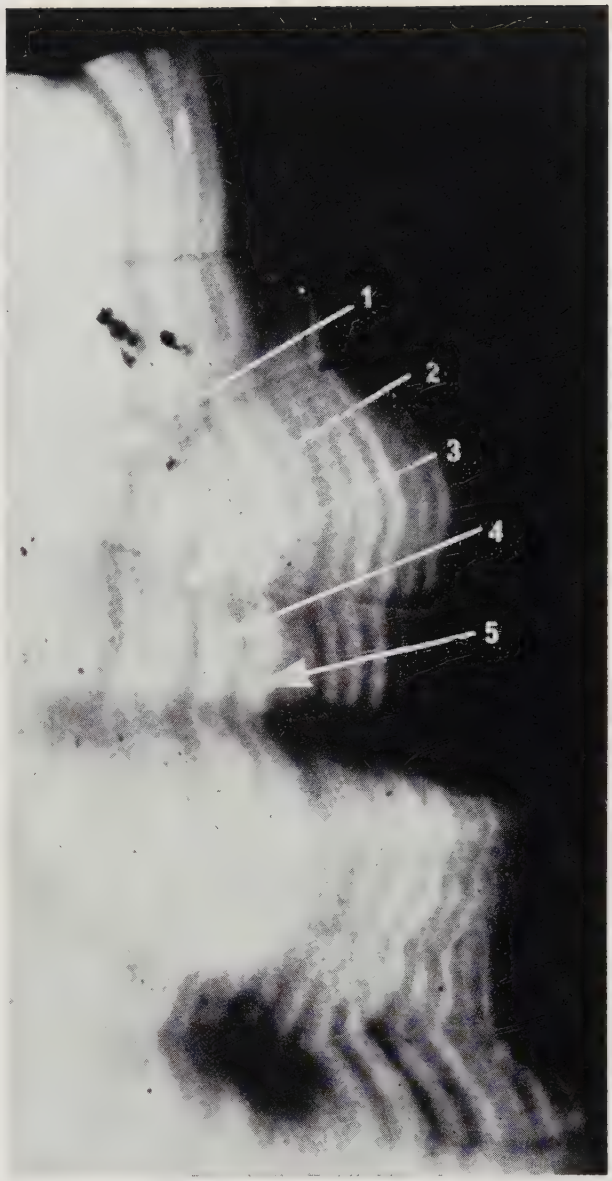


Fig. 4: A tarakihi otolith, showing checks (1, 2, and 3) and double rings (4 and 5). Motiti Island, December 1968.

unimodal between November and July and shifted to higher values during this period, reaching maximal values in May-July. The September distributions showed an abrupt shift to low values, those for ring groups 4 and 5 being bimodal, with a first mode at low values and a second mode in the same position as the July modes. In October ring group 4 showed the same characteristics, but ring groups 5 and 6 were unimodal at low values. In the second December the distributions occurred at slightly higher values and were similar to those found in December 1968. The proportions of m.i. widths of 2 units and less (shaded areas in Fig. 5) decreased from November 1968 onward, became zero in May,

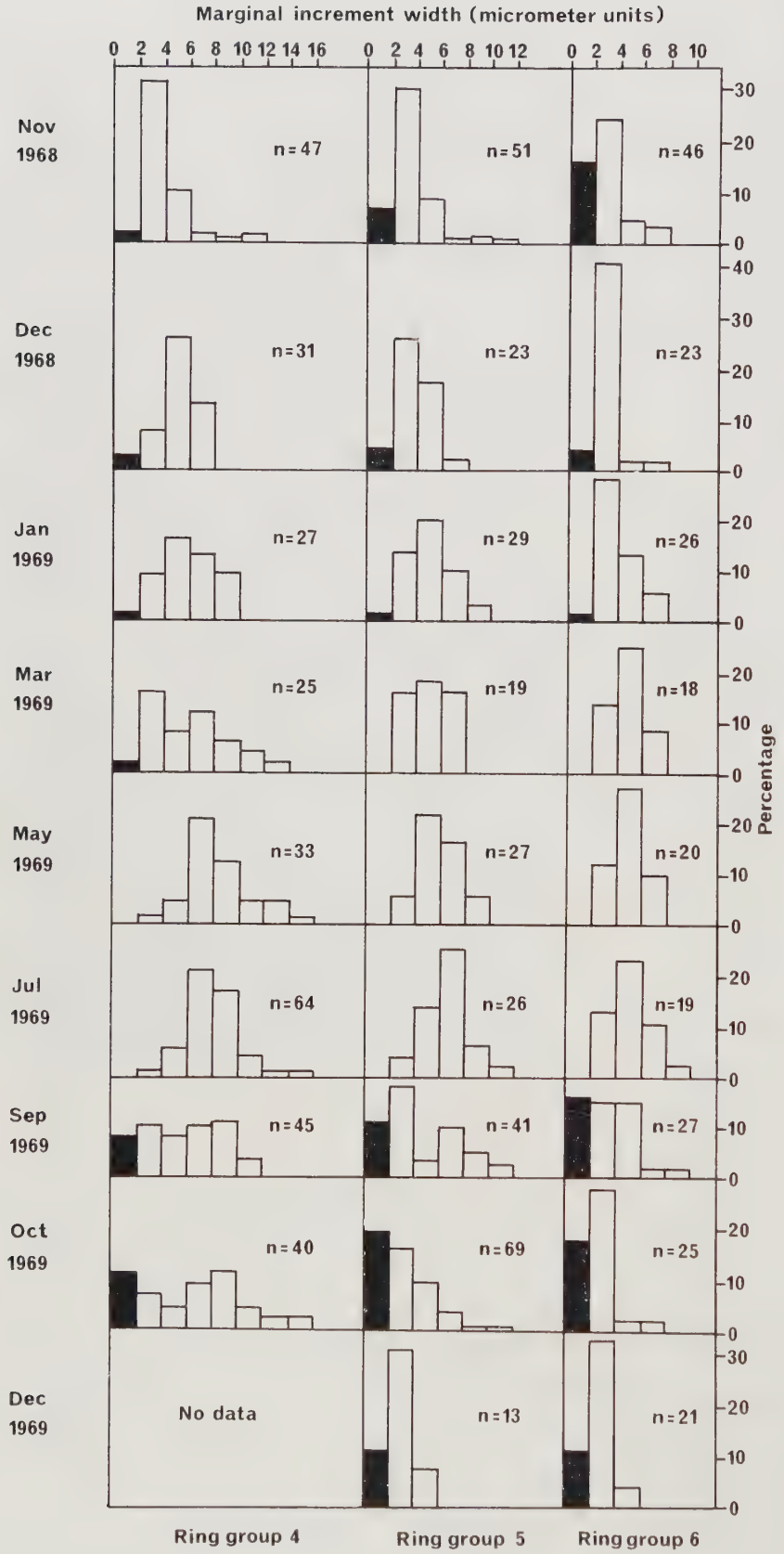


Fig. 5: Marginal increment width-frequency distributions of the combined Bay of Plenty samples. Shaded areas indicate the proportion of otoliths with m.i. width of 2 units or less.

and were maximal in the following September and October.

These results indicate a cyclic fluctuation in m.i. width in the population as a whole, with a period of 1 year, the maximum being in July and the minimum in September. This means that one opaque and one hyaline zone are formed annually. The occurrence of the last hyaline very close to the edge of the otolith in September indicates that the formation of opaque material starts between late July and mid-September. The hyaline material must be laid down at the end of the cycle, during March-July. The present method cannot show more exactly when the formation of the hyaline layer takes place, as the width of a hyaline margin and of the opaque zone inside it are measured together as the m.i. width.

The bimodality of the m.i. width distributions in ring groups 4 and 5 in spring indicates that the formation of opaque material does not start simultaneously in all fish. The narrow m.i.'s in the first mode consist of opaque material formed since the previous winter, and the wide m.i.'s in the second mode consist of a complete opaque zone formed during the previous summer plus a hyaline zone formed in the previous winter. A few m.i.'s of the latter type are still found in November (Fig. 5).

The bimodality of the distributions in spring is not due to sexual differences. For any ring group the m.i. width-frequency distributions of both sexes show no evidence that the modes in the distributions of the ring group as a whole represent separate sexes (Fig. 6).

Comparison between Ring Counts and Petersen's Method

Length-frequency distributions of catches of adult tarakihi taken on the commercial fishing grounds have never been found to show modes indicating individual age groups. Those of catches of small juvenile tarakihi taken on nursery grounds, on the other hand, usually display two or more very distinct modes. Figure 7 shows the pattern on one particular sampling station in Tasman Bay over a series of months. In February 1969 two major modes, A and B, were present, which indicated the existence of two groups of fish, which dominated the catches during the whole following year. Between February and June 1970 a new class of fish arrived in the area and appeared in the June sample as mode C.

Figure 7 shows that the difference between the two consecutive modes A and B in February 1969 was 8 cm, which is almost equal to the average growth of mode A fish between February 1969 and February 1970 (7.5 cm). The same is observed for the June samples of both years: the growth of mode A over the year was 5 cm; the difference between A and B in 1969 was 6 cm. These results indicate that A and B represent two consecutive year classes. In June 1970 the modal length of C was equal to that of A in June 1969, and the difference between C and A in June 1970 was similar to that between B and A 1 year before—5 and 6 cm respectively. Thus if A is 1 year younger than B, C is 1 year younger again than A. Consecutive length-frequency modes represent separate and consecutive age groups; Petersen's method is therefore applicable to juvenile tarakihi samples.

It is not known where and when the spawning takes place from which the Tasman Bay juveniles originate. Ripe tarakihi have been taken on the east coasts of New Zealand from January to June, fish in the higher latitudes spawning earliest (chapter 4). Tasman Bay is in an intermediate position, so that the birth date of the fish there probably falls in the first quarter of the year. The small juveniles with modal length below 10 cm which invade Tasman Bay during that period have probably been spawned in the year previous to their appearance. The modes A, B, and C in Fig. 7 therefore represent the year classes 1968, 1967, and 1969 respectively.

The otoliths of samples of juveniles from the North Otago coast, from Hawke Bay, and from Tasman Bay-Golden Bay were examined. In all these fishes the consecutive ring groups closely coincided with the consecutive modes in the length-frequency distributions and therefore with the age groups (Fig. 8). Thus for the juveniles the same pattern was found as for the adults: one opaque and one hyaline zone together represent 1 year in the life of the fish.

For fish of similar modal length the number of "inside rings" in the North Otago sample (Fig. 8a) was consistently one higher than in the Hawke Bay (Fig. 8b) and Tasman Bay-Golden Bay (Fig. 8c) samples. In the latter two samples, which were collected in June, the otoliths showed wide m.i.'s, but in the North Otago sample, which was collected in November, almost all m.i.'s were very narrow. This difference indicates that opaque material starts to form between June and November. It is likely that the starting date falls in spring, as for the adults, and that the hyaline zone is similarly formed in autumn-winter.

The first mode in the Tasman Bay-Golden Bay sample of Fig. 8 corresponds with mode C in Fig. 7. In June 1970, when these fish were about 1.3 years old, their otoliths showed no inside rings; that is, no hyaline ring was present inside the edge of the

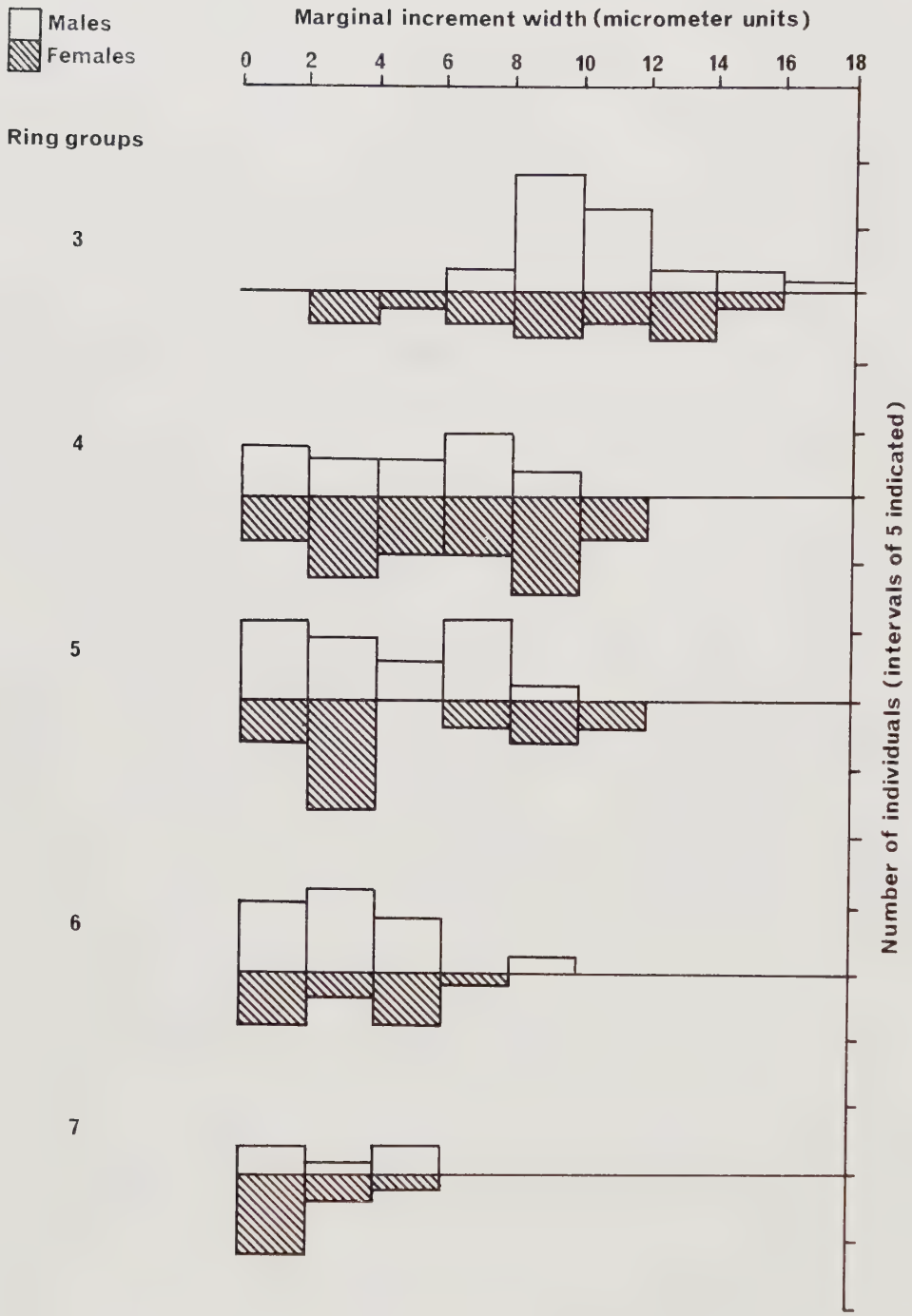


Fig. 6: Marginal increment width-frequency distributions of the sexes within ring groups. Bay of Plenty, September 1969.

otolith. The same was found in the otoliths of Hawke Bay fish of a similar size class collected in June 1969. The fish in the first mode of the North Otago sample, which were spawned in the early part of 1968 and were therefore almost 2 years old, showed one hyaline ring on the otolith. This indicates that in the tarakihi no hyaline ring is formed during the first winter; the first hyaline ring is laid down during the second winter.

AGEING

Tarakihi spawn in the Bay of Plenty between March and July (chapter 4). We have chosen 1 March as the birth date of the year classes for that area, so that age groups correspond with the actual age of the fish; age group n includes fish between n and n + 1 years old. The nucleus and the first hyaline ring represent together the first

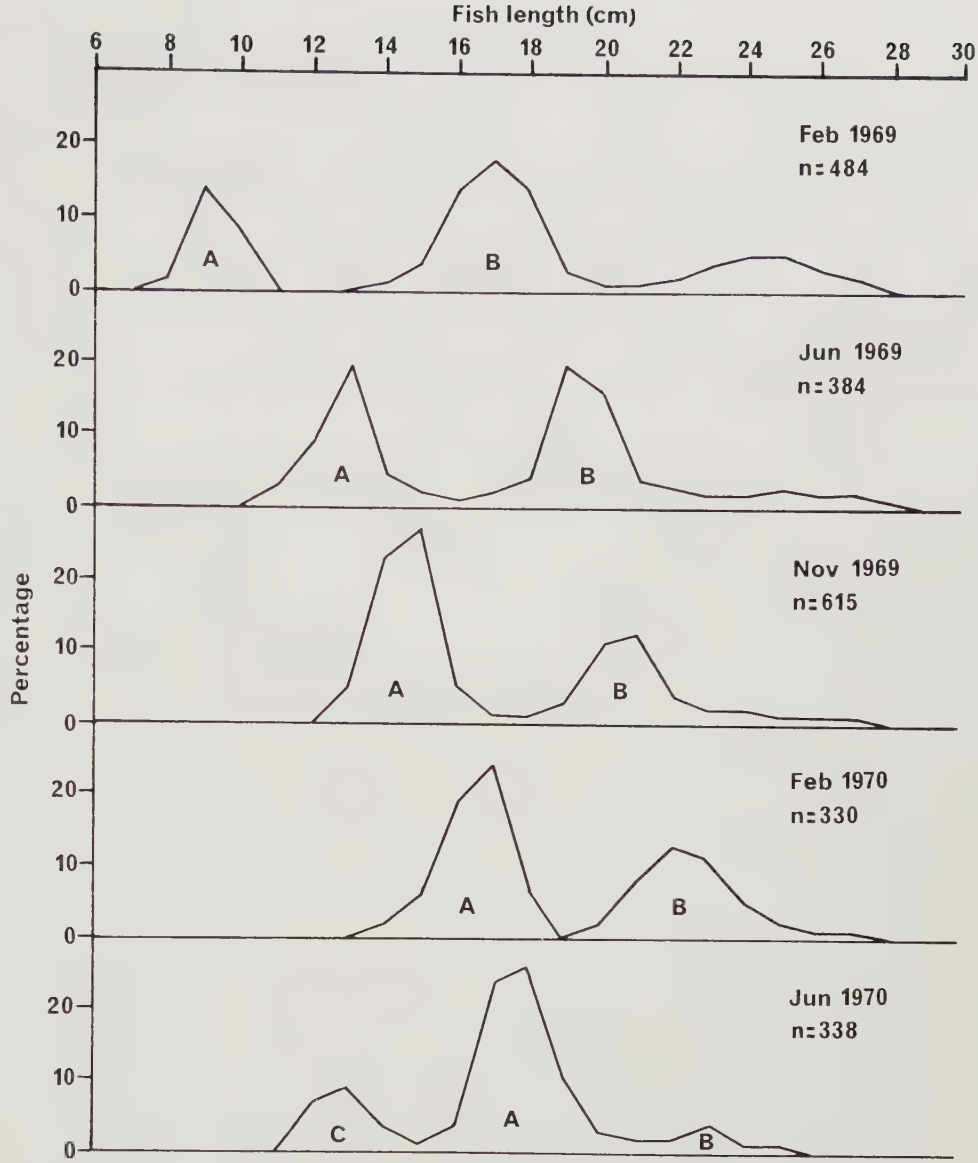


Fig. 7: Length-frequency distributions of a series of samples from a single station in Tasman Bay.

winter, first summer, and second winter in the life of the fish, a period of about 1.5 years. Each subsequent complete set of one opaque and one hyaline zone adds 1 year to the age of the fish, and finally the time involved in the formation of the m.i. must be included.

In spring a distinction must be made between wide m.i.'s, which represent a full year's growth, and narrow m.i.'s, which represent a growth of a few weeks or months. If we consider ring group n in early spring, the fish with narrow m.i. belong to age group n and are n + ½ years old (Fig. 3a), and those with wide m.i. belong to age group n + 1 and are n + 1½ years old (Fig. 3b). The combined results for adults and juveniles indicate that the zone formation follows the same pattern in widely separated areas, so that the above interpretation can be generally used if adjustments for local differences in spawning time are made.

The two age groups within a ring group in spring can be distinguished by measuring the m.i.'s of the ring group and comparing its m.i. width-frequency distribution with the one in winter. The spring distribution can then be divided into two overlapping unimodal distributions, of which the second has to be similar to the winter distribution; this is facilitated if the overall spring distribution is bimodal.

An alternative method not needing measurements, and therefore much quicker, is to interpret each otolith directly by comparing by eye the width of the m.i. with the width of the preceding opaque zones. This was done for the September 1969 samples from the Bay of Plenty, independently from the m.i. measurements. Figure 9 shows the m.i.

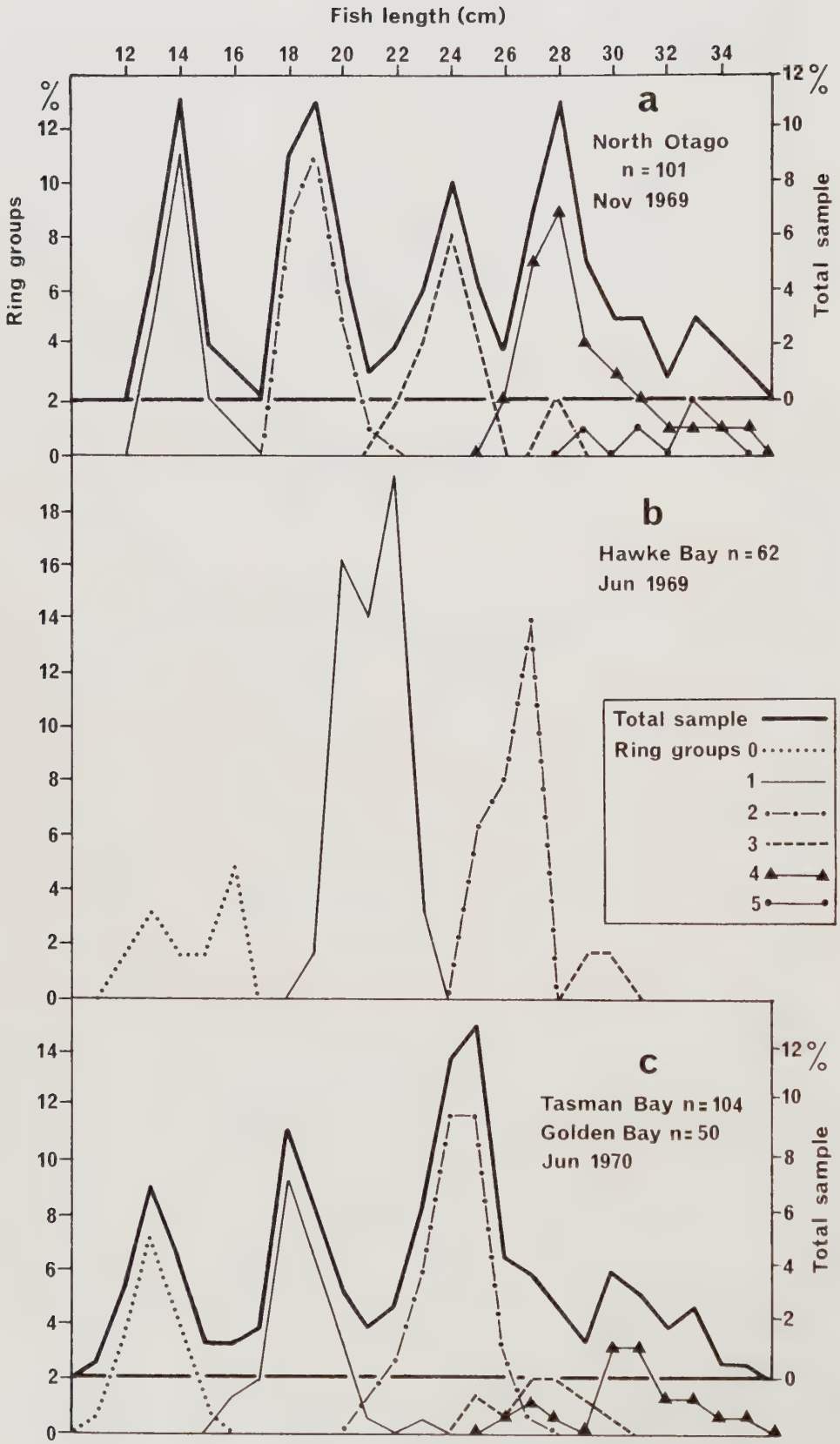


Fig. 8: Length-frequency distributions of total samples (bold lines) and of ring groups (light lines and dotted lines), plotted as percentages of the total sample. The graphs of the total sample and those of the ring groups have different origins.

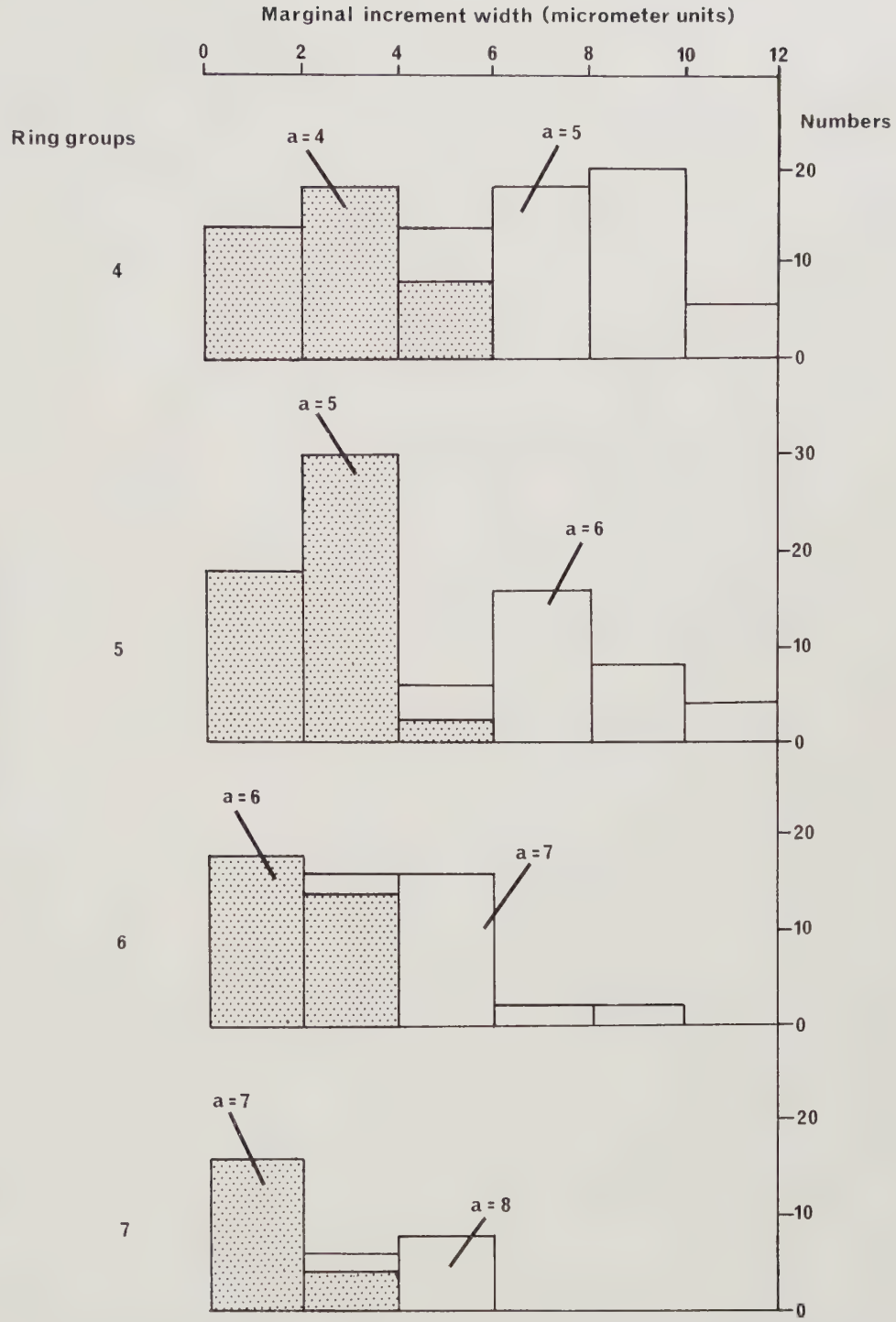


Fig. 9: Results of age determination of a spring sample (Bay of Plenty, September 1969). The histograms show the overall m.i. width-frequency distributions of ring groups 4 to 7. The shading indicates the m.i. width-frequency distributions of the two age groups occurring within each ring group as identified by eye (a: age group).

width-frequency distribution of the resulting age groups within the ring groups 4 to 7. The direct age readings subdivide the ring groups into two overlapping unimodal distributions, and a comparison with Fig. 5 shows that the modal value of the second of each pair of resulting distributions is equal to the modal value of the corresponding July distributions. The direct age readings by eye therefore appear to have separated the ring groups correctly into the fish in which the formation of opaque material has begun recently and those in which it has not. This shows that an experienced observer can interpret spring otoliths reliably by eye without measurements.

Ageing the juvenile sample from North Otago in this way shows that the length-frequency distributions

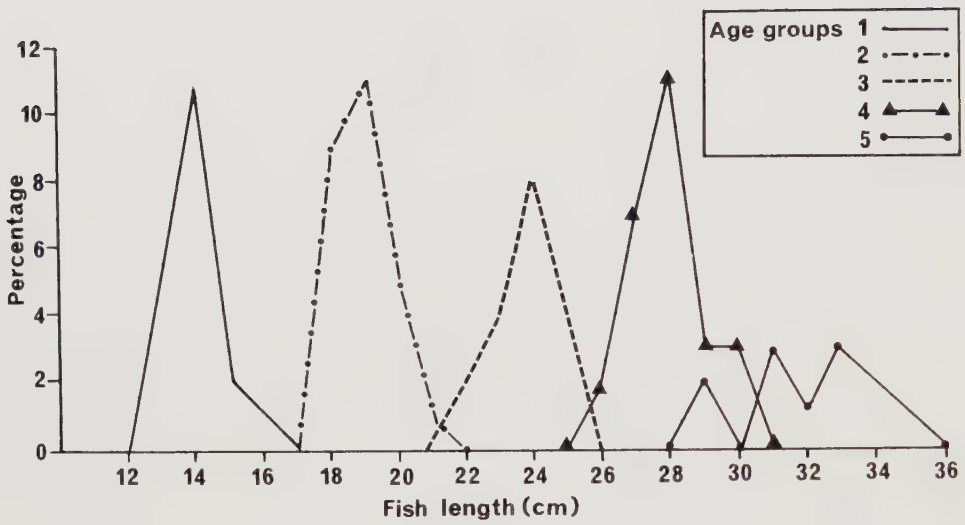


Fig. 10: Length-frequency distributions of age groups, as determined from rings and m.i. widths, plotted as a percentage of the total sample. North Otago, November 1969 (n = 101).

of age groups 3, 4, and 5 overlap far less than those of the corresponding ring groups (Figs. 8a and 10). The overlap between the ring groups is largely due to the presence of some otoliths with wide m.i.'s in ring groups 4 and 5.

ZONE FORMATION AND AGE

The "recent layer" of the otolith is the layer of material formed since the preceding winter only; in summer this consists of a single opaque zone and in winter of an opaque and an outer hyaline zone (checks not being considered). The width of the recent layer of otoliths with wide m.i.'s occurring in spring samples is by definition zero. In all others the m.i. width indicates directly the width of the recent layer. The monthly mean width of the recent layer, as defined in this way, was calculated for the age groups 3 to 7 in the combined Bay of Plenty samples. The results are shown in Fig. 11; the data have not been placed in chronological order, but have been arranged as starting from March to enable the data for any age group to be plotted as one series. The December values for age groups 5 to 7 are the data for December 1968 and 1969 combined.

In the Bay of Plenty first sexual maturity is at 4 years of age and full maturity occurs at 5 and 6 years of age for males and females respectively (chapter 4). Figure 11 shows that the periodicity of zone formation was the same in immature and mature age groups, the maximum being reached in May-July followed by minimal values in September. The graph also shows that especially in autumn-winter the width of the recent layer was clearly inversely proportional to age. This illustrates what has been stated in the general description of the otolith regarding the gradual decrease in zone width from the centre outward.

There is no indication that in the Bay of Plenty within the age range observed (3 to 8 years) the starting date of formation of opaque material in spring varies with age. However, the age groups in the spring sample from North Otago (Figs. 8a and 10) differed in otolith edge characteristics, a narrow but clear recent layer being present in all fish of age groups 1, 2, and 3, but absent in 8 percent of age group 4 (26 fish examined) and 55 percent of age groups 5 (11 fish examined). This indicates that at least in some areas formation of opaque material at the otolith edge starts in young fish earlier in spring than in older fish. This point has to be considered when the ages of fishes collected in spring are determined from otoliths.

The ring groups 4, 5, and 6 shown in Fig. 5 are 5, 6, and 7 years old respectively in March. Ring group 4 is therefore a heterogeneous group, consisting of immature fish and fish that spawn for the first or second time (chapter 4). Usually there is an inverse relationship between gonad growth rate and somatic growth rate in fishes (Nikolskii 1969, pp. 84 and 87). A similar relationship may exist between these two growth rates in the tarakihi and may be reflected in the zone formation on the otolith. This could account for the large variance in the m.i. width data for ring group 4 in March in comparison with those for ring groups 5 and 6, which are more homogeneous in gonad development.

ZONE FORMATION IN DIFFERENT SEA AREAS

In September 1969 results from two of the Bay of Plenty sampling areas differed considerably in the

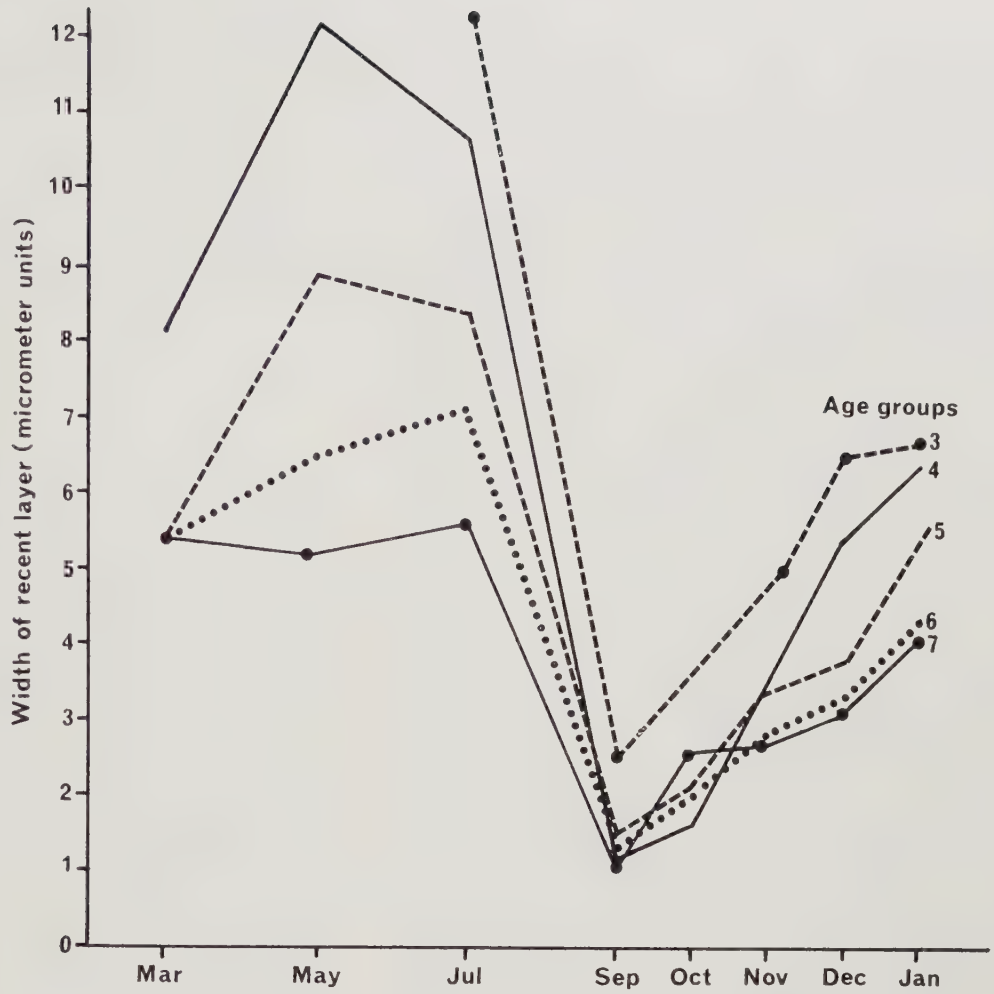


Fig. 11: Monthly mean width of "recent layer" on the otoliths of age groups 3 to 7. Bay of Plenty, 1968–69 (combined samples).

proportion of otoliths with a narrow, recently formed opaque m.i. (Table 1). In September most of the fish from the relatively shallow and in-shore Motiti Island station showed a narrow m.i., whereas most fish from the deeper and more off-shore Plate Island station had wide m.i.'s, which indicated that the formation of opaque material had not yet started there. The Slipper Island sample was intermediate in this respect. In the following October the samples were no longer different.

COMPARISON OF OTOLITH READINGS

"Reading" otoliths is defined as examining otoliths by eye and interpreting the observed pattern directly in terms of age of fish. Five otolith samples from the Bay of Plenty were read independently by both authors without much previous discussion, but both used the basic interpretation described in the section on age determination. The readings did not agree very well (Table 2). The agreement for sample 5, which had been collected in spring, was of the same degree as that for the other samples, which shows that the interpretation of the m.i. in spring otoliths did not present special difficulties.

TABLE 1: Percentages of tarakihi showing narrow m.i. in samples from three stations in the Bay of Plenty, with 95 percent confidence limits of estimates in parenthesis

	Motiti I.	Slipper I.	Plate I.
September 1969	78 (±10)	44 (±19)	22 (±9)
October 1969	72 (±13)	85 (±11)	67 (±9)

After a discussion of the various otolith structures observed, the samples were again read independently, and agreements ranging from 72 to 93 percent were found (Table 2). The results for sample 4, plotted in detail in Fig. 12, show certain features that were found in all samples. The differences between the first readings were mostly 1 or 2 years. This indicates that the disagreements were due to minor differences in observation or interpretation. Initial disagreement was highest between the higher readings, which indicates that the interpretation of the otoliths becomes more difficult as the age of the

TABLE 2: Comparison of otolith readings by two readers

Sample No.	Sample date	Sample size	Age range	Number unreadable	% agree 1st reading	% agree 2nd reading
1	December 1968	96	1–20	2	74	93
2	March 1969	73	3–15	1	53	72
3	May 1969	65	4–16	1	39	77
4	May 1969	67	1–20	1	45	89
5	October 1969	108	3–20	2	40	81

fish increases. In the first readings reader A tended to read lower than reader B. In sample 4, for instance, A read 22 times lower and 14 times higher than B. This difference disappeared the second time, and the few remaining disagreements in interpretation were mainly 1 year. These improvements in the results were due to the use of more precise definitions of checks and "double rings" and consistent examination of both otoliths entirely. During the first readings this examination of both was not usually done. The otoliths of a pair show basically the same pattern, but sometimes one is clearer than the other.

In some otoliths the zones were so poorly marked that any age interpretation was a mere guess. Such otoliths were classed as "unreadable". Table 2 shows that between 1 and 2 percent of the otoliths fell into this category.

Estimates of the age compositions and of the mean length per age group of the sampled population were made by using the two independent second readings of sample 5. Table 3 shows that the differences between the estimates are almost all minor; in the few appreciable differences the 95 percent confidence intervals of the estimates still overlap considerably. The differences between the estimates of the variances of the length within the age groups, as indicated by the magnitude of the confidence limits, are also mostly small.

DISCUSSION

Two major zones are formed annually on the tarakihi otolith. A wide opaque zone is laid down in spring-summer and a narrow hyaline zone in autumn-winter. In addition, irregular hyaline checks may occur in the opaque summer zones. This general pattern occurs in the juvenile as well as in the mature fish. At the onset of sexual maturity the overall pattern is only quantitatively modified, in so far as the rate of somatic growth changes in relation to the gonad growth.

Fish otoliths consist mainly of calcium carbonate in the form of aragonite (76.39 percent in otoliths of cod, *Gadus morhua* L.), with some calcium oxide and organic material, the latter amounting to 0.2 to 10.0 percent (Dannevig 1956, Degens, Deuser, and Haedrich 1969). The fact that the wide otolith zones are formed in the tarakihi in spring-summer indicates that during those seasons the rate of calcification is much more rapid than in autumn-winter, when narrow zones are formed. The formation of opaque material coincides with rapid calcifica-

TABLE 3: Estimates of age composition and mean length per age, based on independent readings of sample 5 (see Table 2) by two readers

(The 95 percent confidence intervals of the estimates are given in parenthesis. Those for age composition estimates are taken partly from Arkin and Colton (1964) and those for estimates of mean length are given only for samples larger than 2.)

Age (years)	Percentage age composition, reader A	Percentage age composition, reader B	Mean length, reader A (cm)	Mean length, reader B (cm)
3	1 (0.2–6.5)	1 (0.2–6.5)	31.0	31.0
4	6 (2.2–12.6)	5 (1.6–11.3)	28.8 (±2.0)	29.8 (±2.5)
5	14 (7.9–22.9)	15 (8.7–23.5)	32.9 (±1.1)	32.2 (±1.2)
6	9 (4.2–16.4)	8 (3.5–15.2)	32.5 (±1.0)	32.8 (±1.2)
7	13 (7.2–21.2)	16 (8.7–23.5)	34.5 (±1.0)	34.7 (±0.9)
8	23 (14.8–31.2)	22 (13.8–30.2)	35.4 (±0.6)	35.3 (±0.6)
9	16 (8.7–23.2)	14 (7.9–22.4)	35.5 (±0.5)	35.5 (±0.6)
10	4 (1.1–9.9)	5 (1.6–11.3)	36.3 (±1.5)	36.6 (±0.7)
11	5 (1.6–11.3)	4 (1.1–9.9)	36.0 (±2.8)	35.8 (±4.0)
12	4 (1.1–9.9)	4 (1.1–9.9)	36.3 (±4.6)	36.5 (±4.2)
13	0	1 (0.2–6.5)	—	34.0
14	1 (0.2–6.5)	1 (0.2–6.5)	39.0	39.0
15	3 (0.6–8.5)	1 (0.2–6.5)	38.7 (±1.4)	39.0
16	0	1 (0.2–6.5)	—	38.0
17	1 (0.2–6.5)	1 (0.2–6.5)	39.0	39.0
18	0	1 (0.2–6.5)	—	39.0
19	1 (0.2–6.5)	0	40.0	—
20	0	1 (0.2–6.5)	—	40.0

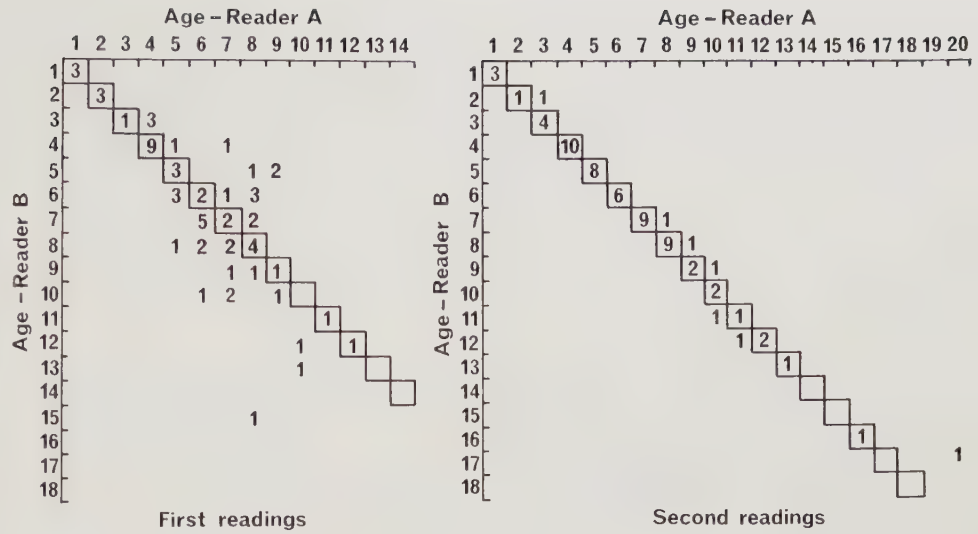


Fig. 12: Comparison of repeated otolith readings by two observers, for sample 4 (see Table 2), plotted in the manner used by Kohler (1964). The agreements are shown by the numbers inside the squares.

tion, and when calcification is slow, hyaline material is laid down.

The fact that the centre of the tarakihi otolith is hyaline and that the first hyaline ring is formed during the second winter in the life of the fish recalls similar patterns found in the hake, *Merluccius merluccius*, which spawns most intensively in mid-summer in the Northern Hemisphere (July), and in the autumn-spawning Icelandic and North Sea herring, *Clupea harengus* L. (Hickling 1930, 1933, Einarsson 1951, Parrish and Sharman 1958, Raitt 1961). As the tarakihi also spawns in late summer and autumn, these otolith characteristics may well be generally associated with summer- and autumn-spawning habits. Spring-spawning fish, such as the Icelandic spring herring, *Clupea harengus*, and the North Sea sprat, *Clupea sprattus* L., have opaque otolith centres and form their first hyaline zone during their first winter (Einarsson 1951, Iles and Johnson 1962).

The difference in transparency between the opaque and hyaline otolith zones appears to be due to a difference in the amount and density of organic material present, though the published evidence does not agree on which type of zone contains the most organic matter (Hickling 1933, Blacker 1969). It is as yet not understood what mechanism causes the periodic changes in the structure of fish otoliths. Graham (1929) and Hickling (1930) suggested that they reflect metabolic changes, hyaline material being formed when anabolism is low and opaque material when it is high. These metabolic changes would result from interactions between fish behaviour (for example, spawning and migration) and environmental factors such as food and temperature. Irie (1960) has shown experimentally that the calcification rate of the otolith is strongly positively correlated with water temperature and amount of food available. In areas of the Bay of Plenty that are not very far apart the time at which the formation of opaque material starts on the otoliths of the tarakihi may differ by as much as 1 month. The distance between the Motiti Island and Plate Island stations, where this was observed, is about 9 km. Both stations have a similar smooth sandy bottom, but they differ much in depth, the former station being 60 to 70 m deep, the latter 150 to 200 m. In early spring there is no difference in bottom temperature between these two depth zones in the Bay of Plenty (P. E. Roberts, pers. comm.), but there are differences between the two stations in the food available, not only in spring but throughout the year (B. L. Godfriaux, pers. comm.). These differences may account for the variation in otolith growth in spring.

The zonation pattern on tarakihi otoliths is sufficiently clear to establish well-defined criteria for the interpretation of the zones. Using these criteria, two experienced observers reached agreements of 72 to 93 percent between independent age readings of samples. These results compare favourably with the figures on cod otoliths presented by Kohler (1964), which ranged between 48 and 84 percent. The differences between the estimates of age composition, of mean length per age, and of the variance of the length within age groups were found to be correspondingly small. These results indicate that the age of individual tarakihi can be reliably determined from the zonation pattern of the otolith, which thus provides one of the basic requirements for further study of the population dynamics of this species.

CHAPTER 3

AGE AND GROWTH

By C. M. Vooren

MATERIAL AND METHODS

From November 1968 to December 1969 samples of tarakihi were collected at regular intervals by trawling near Motiti Island, Plate Island, and Slipper Island (Table 4). The sampling localities, the gear used and the methods of sampling, fish length measurement, and age determination are described in chapter 2. The birth date of the year classes in this region has been taken as 1 March (see page 20). The whole body weights of the fish were measured to the nearest 5 g with a Salter No. 159 balance having a weighing capacity of 2,000 g.

Tests of significance referred to in this chapter were made according to Tables 13 and 22 in Arkin and Colton (1964).

AGE COMPOSITION

The age composition of the samples is shown in Fig. 13. The age of the fish ranged from just over 1 year (Motiti Island, May 1969) to almost 26 years (Slipper Island, January 1969). Most fish were between 3 and 9 years old. Fish of less than 6 years old were more strongly represented near Plate Island, and fish of more than 6 years old were more abundant in autumn near Motiti Island, than at other times of the year. Apart from this there is no clear pattern in the considerable variation between the samples.

Age groups 0 to 2 were almost absent in all samples. This absence of small juveniles is a persistent feature of all trawling grounds in the Bay of Plenty (Tong and Elder 1968). The possibility that these juveniles might occur on rough ground where trawling is impossible was investigated repeatedly in the course of the present study by line fishing on such grounds near Motiti Island and Slipper Island, but the results were always negative. Several tarakihi nursery areas have recently been found around the South Island of New Zealand, all at moderate depths on the Continental Shelf (Vooren in prep.); so there is no reason to assume that in the Bay of Plenty the juveniles are pelagic or occur outside the edge of the Continental Shelf. It can therefore be concluded that there is no tarakihi nursery ground in the Bay of Plenty and that recruitment must take place through migration from elsewhere.

SEASONAL GROWTH

The monthly mean lengths of age groups 4 to 9 were plotted as one series, the birth date of the year classes being taken as the start (Fig. 14). The graph suggests that growth took place mainly in September-January and April-May and that there was little growth in February-March and June-August. This pattern was clearest in age groups 4 to 6. Thus it seems that there are two bursts of growth—a major one in spring-summer and a minor one in autumn.

The cessation of growth in late summer-early autumn coincides with the rapid increase in gonad weight before spawning (see page 39) and may therefore be connected with spawning.

The "double rings" occurring in otoliths of some of the mature fish (see page 16) may reflect this seasonal growth pattern.

TABLE 4: List of sampling dates

Year	Station	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1968	Motiti I.	—	—	—	—	—	—	—	—	—	—	12	10
	Slipper I.	—	—	—	—	—	—	—	—	—	—	13	9
1969	Motiti I.	14	—	10	—	22	—	22	—	16	7	—	1
	Slipper I.	13	—	—	21	21	—	23	—	17	6	—	2
	Plate I.	—	—	10	23	22	—	22	—	16	7	—	—

A dash indicates that no sample was collected.

ANNUAL GROWTH

The samples collected in January, March, July, and September 1969, representing summer, autumn, winter, and spring respectively, were subjected to an analysis of variance of the length-at-age between the sampling stations and between the sexes. Only the data for the most abundant age groups—5 to 7—were used. In 11 tests the differences between the stations and between the sexes were significant only four and three times respectively (Table 5). No differences were significant for all age groups considered.

The samples collected in March, April, May, and July 1969 were combined and treated as one sample for a further growth analysis.

An analysis of variance of the sets of data thus obtained revealed highly significant differences

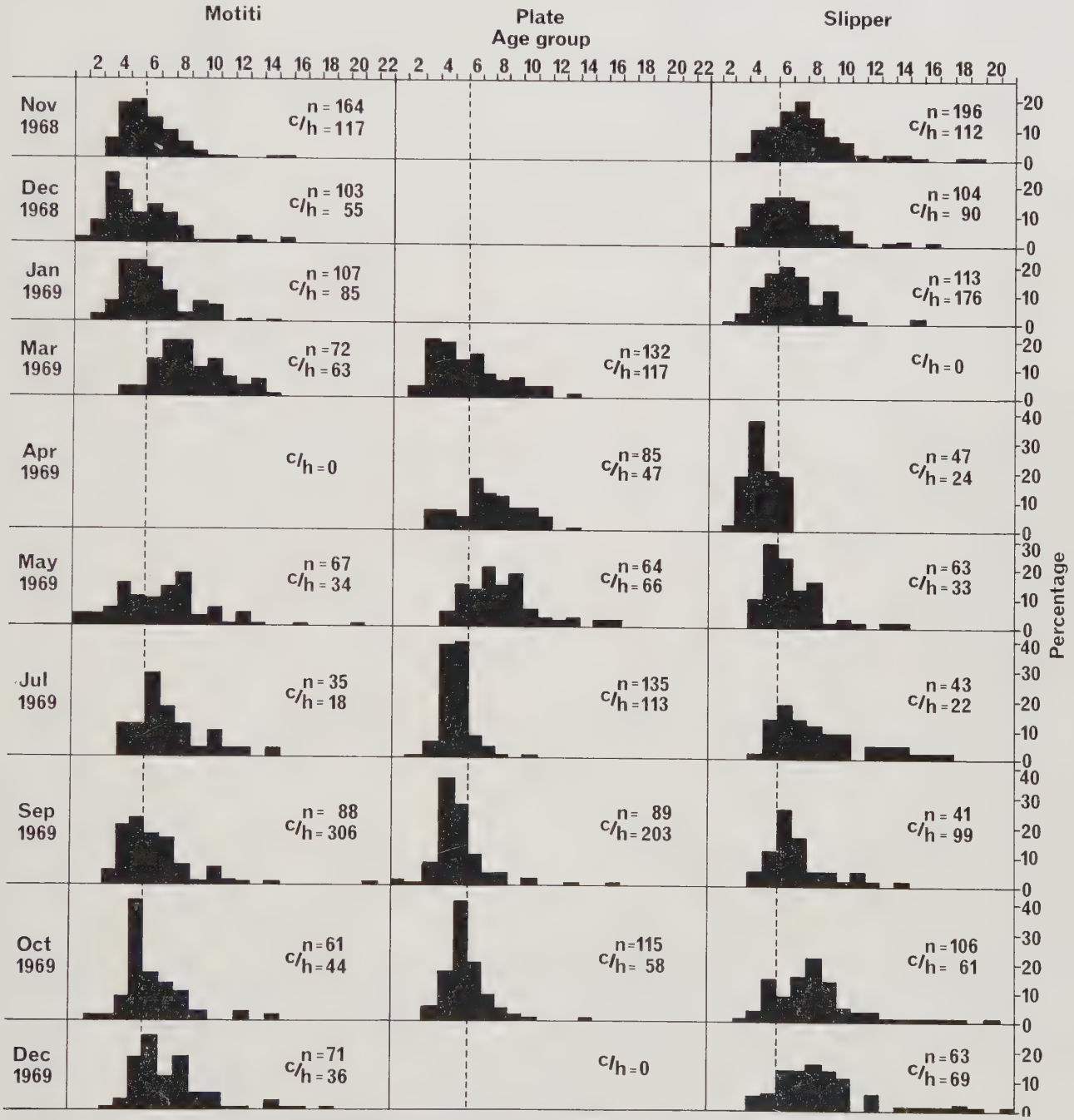


Fig. 13: Age composition (percentage) and fish density (expressed as catch/hour trawling) at all sampling stations; n is sample size and c/h is catch/hour trawling in numbers. Broken lines separate age groups 5 and 6.

TABLE 5: Analysis of variance of length of age groups 5 to 7, between sampling stations and between sexes, for individual months

Stations	Month	Age group	F between stations	F between sexes
Slipper I., Motiti I.	January 1969	5	17.6534 at 40 and 1 d.f.	5.9904 at 40 and 1 d.f.
Slipper I., Motiti I.	January 1969	6	4.1750* at 1 and 39 d.f.	5.8121* at 1 and 39 d.f.
Slipper I., Motiti I.	January 1969	7	4.2206* at 1 and 28 d.f.	11.0208** at 1 and 28 d.f.
Plate I., Motiti I.	March 1969	6	2.0457 at 26 and 1 d.f.	1.2099 at 26 and 1 d.f.
Plate I., Motiti I.	March 1969	7	16.6529** at 1 and 22 d.f.	8.0161** at 1 and 22 d.f.
Slipper I., Plate I., Motiti I.	July 1969	5	2.6641 at 2 and 60 d.f.	1.7148 at 60 and 1 d.f.
Slipper I., Plate I., Motiti I.	July 1969	6	3.3530 at 2 and 26 d.f.	3.8260 at 1 and 26 d.f.
Slipper I., Plate I., Motiti I.	July 1969	7	2.6093 at 2 and 13 d.f.	1.4308 at 13 and 1 d.f.
Slipper I., Plate I., Motiti I.	September 1969	5	5.1369* at 2 and 44 d.f.	3.2573 at 44 and 1 d.f.
Slipper I., Plate I., Motiti I.	September 1969	6	1.4045 at 2 and 33 d.f.	8.8652 at 33 and 1 d.f.
Slipper I., Plate I., Motiti I.	September 1969	7	4.2406 at 2 and 21 d.f.	2.1432 at 1 and 21 d.f.

* 5 percent significance.

** 1 percent significance.

F: Test statistic (variance ratio).

d.f.: Degrees of freedom.

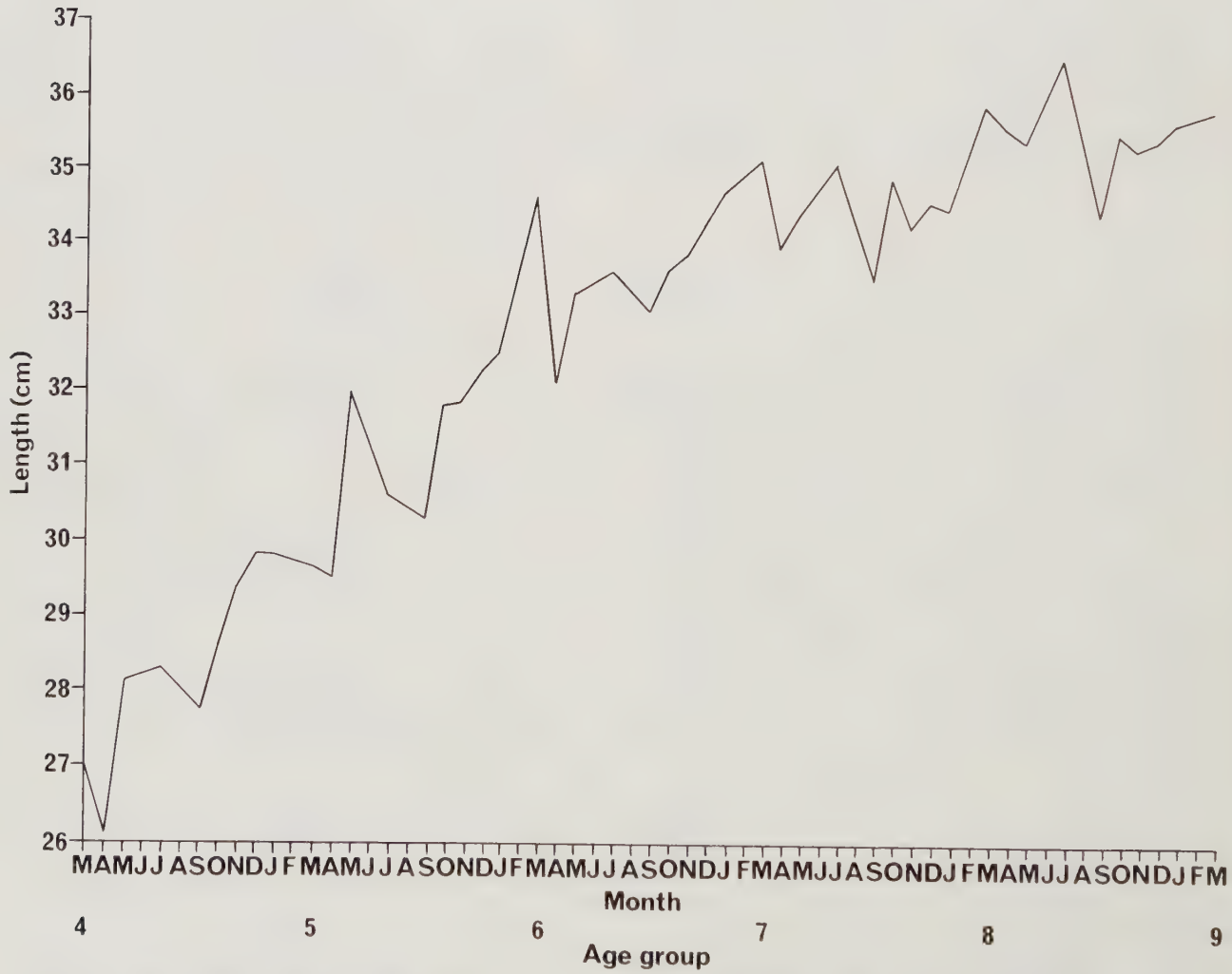


Fig. 14: Monthly mean length of age groups 4 to 9, all stations combined. Values for December are means of December 1968 and December 1969.

TABLE 6: Analysis of variance of length of age groups 5 to 9, between sampling stations and between sexes, for the combined samples of March, April, May, and July 1969

(Symbols as in Table 5.)

Age group	Source	F		
5	Between sexes	42.1941	at 125 and	1 d.f.
	Between stations	3.9206*	at 2 and 125	d.f.
6	Between sexes	8.6489**	at 1 and 108	d.f.
	Between stations	9.3237**	at 2 and 108	d.f.
7	Between sexes	9.2948**	at 1 and 77	d.f.
	Between stations	4.3700**	at 2 and 77	d.f.
8	Between sexes	9.2099**	at 1 and 66	d.f.
	Between stations	5.8828**	at 2 and 66	d.f.
9	Between sexes	3.9606	at 1 and 38	d.f.
	Between stations	1.5997	at 2 and 38	d.f.

between stations and between sexes for age groups 6, 7, and 8. For age group 5 the difference between stations was significant at a lower level, and no significance was found for age group 9 (Table 6). When, however, the sexes were considered separately the differences between the stations disappeared. Significance was then found in only one test and this is regarded as accidental (Table 7).

These results show that in the age groups 6 and older there is a consistent difference in length between the sexes, the females being larger than the males (Table 8). The absence of significance in most tests listed in Table 5 and in the test for age groups in Table 6 indicates that a sample size of about 70 is necessary to show the significance of the difference between the sexes (the sample sizes follow from the degrees of freedom listed in the tables). A similar difference between the sexes has been found in tarakihi near East Cape, where it was shown that this reflects a difference in growth rate (Vooren and Tong in press). The age group 5 in the present samples is just over 5 years old, the birth date being 1 March. Therefore in the Bay of Plenty also, a divergence between the growth patterns of the sexes begins in the sixth year.

Females dominated in the samples from Motiti Island and Slipper Island and males in the samples from Plate Island (Table 7). Hence the mean length of each age group as a whole was significantly lower at Plate Island than at the other two stations. This difference reflects the difference between the sexes; Table 7 shows that the growth rates of the sexes at the three stations were similar.

Individual fish lengths ranged between 12 and 45 cm, and weights between 20 and 1,660 g (Tables 8 and 9). The length ranges of the age groups overlapped considerably; for instance, fish of 37 cm were between 4 and 16 years old.

TABLE 7: Analysis of variance of length of males and females of age groups 6 to 8, between sampling stations, and percentage of females at the stations for the combined samples of March, April, May, and July 1969
(Symbols as in Table 5.)

	Age group	F between stations		Percentage of females		
				Plate I.	Motiti I.	Slipper I.
Males:	6	2.8658	at 2 and 50 d.f.			
	7	2.2353	at 2 and 28 d.f.			
	8	1.4346	at 2 and 25 d.f.			
Females:	6	7.2258**	at 2 and 56 d.f.	32	79	69
	7	1.8322	at 2 and 47 d.f.	41	86	75
	8	3.0403	at 2 and 39 d.f.	19	93	73

TABLE 8: Mean lengths (cm) of the age groups from the samples collected in March-July 1969

Age	Females			Males			Total			
(years)	Sample size	Mean	S.E.	Sample size	Mean	S.E.	Sample size	Mean	S.E.	Range
1	2	—	—	1	—	—	3	12.7	—	12–13
2	4	—	—	4	—	—	9	18.8	0.8	13–20
3	23	—	—	30	—	—	53	23.8	0.3	20–30
4	67	—	—	63	—	—	133	27.5	0.2	23–37
5	64	—	—	67	—	—	133	30.7	0.2	23–37
6	58	34.0	0.3	54	32.8	0.3	114	33.4	0.2	28–40
7	50	35.1	0.3	32	33.8	0.3	84	34.6	0.2	31–41
8	42	36.2	0.3	27	34.8	0.4	74	35.6	0.2	32–40
9	22	36.6	0.4	20	35.4	0.5	43	36.0	0.3	23–40
10	28	37.3	0.5	12	36.3	0.6	41	37.0	0.4	32–41
11	11	38.1	0.5	8	37.1	0.6	19	37.7	0.4	37–42
12	7	39.3	1.2	3	38.0	—	10	38.9	0.9	35–39
13	8	39.0	1.4	4	38.8	1.1	12	38.9	0.3	36–42
14	2	42.0	—	2	37.0	—	4	39.5	1.9	36–45
15	2	39.5	—	1	42.0	—	3	40.3	—	37–42
16	2	40.0	—	1	37.0	—	3	39.0	—	37–43
17	0	—	—	2	38.0	—	2	38.0	—	—
20	1	40.0	—	0	—	—	1	40.0	—	—

S.E.: Standard error of estimate.
A dash indicates that no estimate was made.

TABLE 9: Mean weights (g) of the age groups from the samples collected in March-July 1969

Age	Females			Males			Total			
(years)	Sample size	Mean	S.E.	Sample size	Mean	S.E.	Sample size	Mean	S.E.	Range
1	0	—	—	1	—	—	3	47	—	20–50
2	3	—	—	3	—	—	6	140	11	110–140
3	17	—	—	26	—	—	43	249	10	220–950
4	46	—	—	40	—	—	88	381	13	220–950
5	44	—	—	45	—	—	89	563	9	220–950
6	49	733	27	45	653	18	94	708	13	380–1,220
7	41	806	22	28	749	27	69	806	7	520–1,210
8	38	852	22	25	802	22	68	829	16	690–1,180
9	18	924	46	17	846	27	36	884	27	720–1,370
10	24	994	31	12	932	49	37	932	28	670–1,300
11	10	1,049	57	7	917	58	17	995	43	810–1,320
12	6	1,133	86	2	1,030	—	8	1,108	69	740–1,230
13	6	1,033	70	4	1,048	96	10	1,039	54	840–1,320
14	2	1,325	—	1	780	—	3	1,143	—	780–1,660
15	2	1,190	—	1	1,300	—	3	1,227	—	1,020–1,360
16	2	1,200	—	1	700	—	3	1,033	—	700–1,380
17	0	—	—	2	1,050	—	2	1,050	—	—
20	1	1,010	—	0	—	—	1	1,010	—	—

S.E.: Standard error of estimate.
A dash indicates that no estimate was made.

Although age groups 1 to 3 were incompletely sampled (Table 8, Fig. 13), the estimates of the mean lengths were similar to the modal lengths of these age groups in autumn-winter in other areas (Figs. 7 and 10) and are therefore considered reliable. A similar check was not available for the scarcely represented age groups 15 to 20, which were therefore excluded from the growth analysis.

A smooth growth curve could be drawn through the length data for age groups 1 to 14 (Fig. 15). The curve shows that the annual growth rate decreases sharply after age 5 years. A similar pattern has been found in the East Cape area, but there the growth rate after age 6 years is much higher than in the Bay of Plenty (Vooren and Tong in press).

A Ford-Walford regression (Ford 1933, Walford 1946) fitted the growth data well (Fig. 16). This indicates that the growth can be described by the von Bertalanffy growth equation in the form given by Beverton and Holt (1957):

$$l_t = L_\infty (1 - e^{-K(t - t_0)}).$$

From the Ford-Walford regression the following estimates were obtained:

$$L_\infty = 39.9 \text{ cm}$$
$$K = 0.26$$
$$t_0 = -0.49 \text{ year}$$

The estimate of t_0 is the mean of the estimates for age groups 1 to 10. The individual estimates ranged between –0.98 and +0.05 year (Table 10). The mean t_0 is close to zero, which indicates that the equation provides a reasonable description of the complete growth pattern; for the length at $t = 0$, the equation gives 4.8 cm.

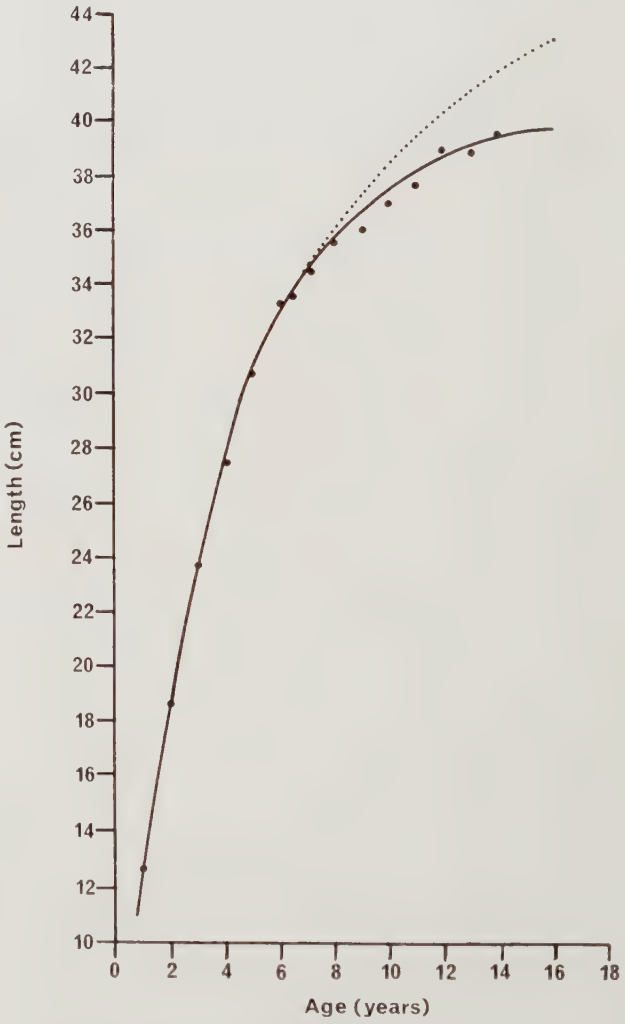


Fig. 15: Growth curves of tarakihi in the Bay of Plenty (solid line) and the East Cape area (broken line). (After Vooren and Tong in press.)

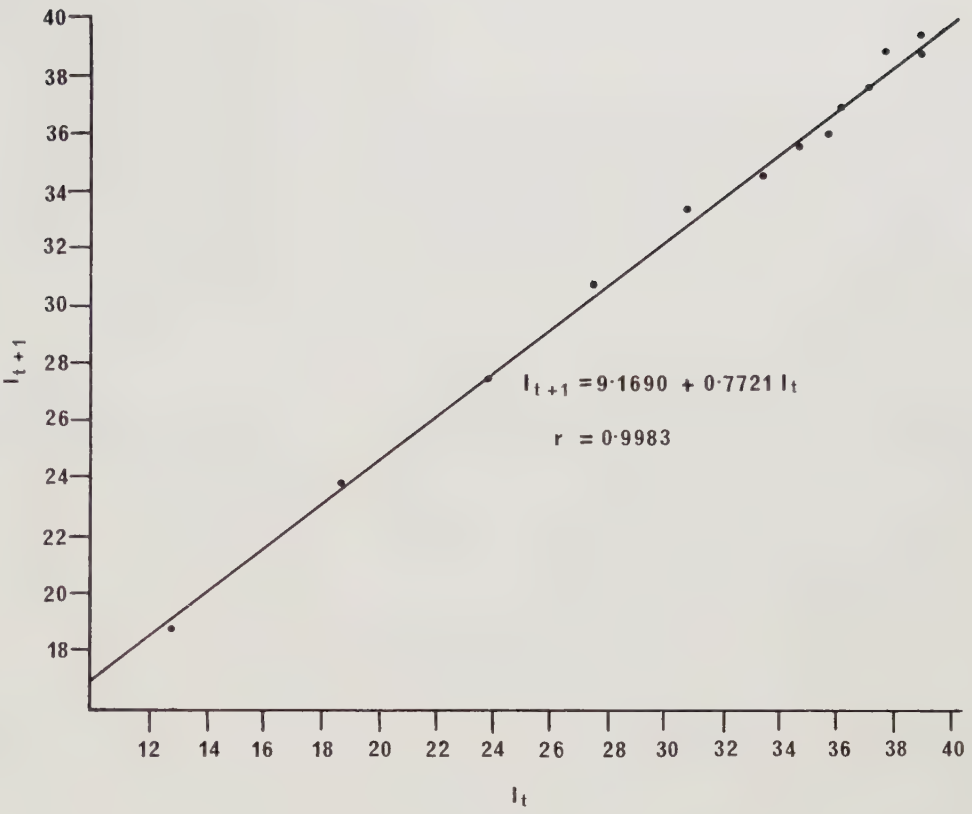


Fig. 16: Ford-Walford regression for age groups 1 to 14, both sexes combined. l is length (cm), t is time (years), and r is correlation coefficient.

The values of the growth parameters differ distinctly from those that have been found in the East Cape area, where L = 50.3 cm, K = 0.1, and t_0 = –4.3 years (Vooren and Tong in press). This states more precisely the difference between the growth patterns in the two areas shown by the growth curves (Fig. 15).

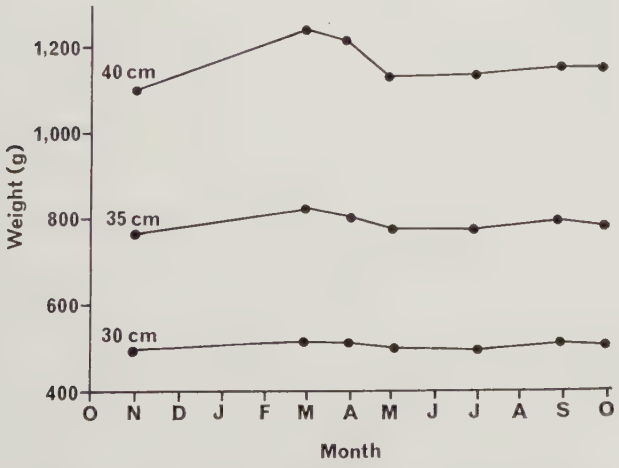


Fig. 17: Monthly mean weights of fish of 30 cm, 35 cm, and 40 cm estimated from equations in Table 2.

LENGTH-WEIGHT RELATIONSHIPS

For the analysis of the relationship between body length and body weight the samples from the three sampling stations were combined for each month.

A high degree of linear correlation was found between the logarithms of weight and length, which indicates that an equation of the type $W = aL^b$ fits the data well (W is weight, L is length, and a and b are constants). The correlation coefficients and equations obtained for each month are listed in Table 11. The values of the exponent ranged between 2.7108 and 3.0869. The whole weight is

TABLE 10: Estimates of t_0

Age (years)	t_0
1	—0.47
2	—0.45
3	—0.49
4	—0.49
5	—0.64
6	—0.98
7	—0.76
8	—0.56
9	+0.05
10	—0.09
Mean	—0.49

TABLE 11: Relationship between body weight and body length

Month	Sample size	r	Equation
November 1968	357	.9672	$W = 0.0500 \times L^{2.7108}$
March 1969	146	.9801	$W = 0.0141 \times L^{3.0869}$
April 1969	126	.9845	$W = 0.0176 \times L^{3.0184}$
May 1969	192	.9853	$W = 0.0300 \times L^{2.8602}$
July 1969	123	.9803	$W = 0.0214 \times L^{2.9511}$
September 1969	129	.9569	$W = 0.0366 \times L^{2.8060}$
October 1969	196	.9528	$W = 0.0280 \times L^{2.8787}$

W: Weight (g).

L : Length (cm).

r : Coefficient of linear correlation between $\log_e W$ and $\log_e L$.

therefore closely proportional to the cube of the length.

From the equations the monthly mean weights of fish of 30, 35, and 40 cm were calculated. As is to be expected with the type of equation found, seasonal variations in the weight for a given length are shown more clearly by the larger fish (Fig. 17). The data show an increase in weight from December to March, followed by a return to the previous level in May. The difference between maximum and minimum weight of fish of 40 cm in both sets of data was about 100 g, that is, 8 percent of the maximum weight.

Spawning takes place in March and April. The data on the gonadosomatic index (see page 39) indicate that the increase in body weight during that period is largely, but not entirely, due to the increase in gonad weight.

CHAPTER 4

BREEDING BIOLOGY

By L. J. Tong

INTRODUCTION

Little published information is available on the breeding biology of the tarakihi. McKenzie (1961) and Han (1964) deal with some aspects in their short reports, and Angot (1951) gives observations on spawning at Amsterdam and St. Paul Islands. Graham (1939) refers briefly to spawning in Otago waters.

The present chapter and that of the complementary study on gametogenesis (chapter 5) set out some of the recent basic studies made on the breeding biology of the New Zealand tarakihi in the Bay of Plenty. These data will provide background knowledge for more routine and regular studies over a much wider area of New Zealand's Continental Shelf.

MATERIAL AND METHODS

Between April 1967 and July 1968 cruises were made to the Bay of Plenty at approximately monthly intervals to sample tarakihi at three stations—in Mercury Bay, north of The Aldermen Islands, and off Motiti Island (Fig. 1). The average depth at each station was 84 m, 144 m, and 79 m respectively. Samples were caught with an otter trawl with a 60-ft (18.3-m) ground rope and for all but two sampling periods a $1\frac{1}{2}$-in. (3.8-cm)-mesh liner was placed in the cod-end. Tows lasted from 1 to 4 hours. When possible, a sample of 100 fish was taken at random from the catch, or the whole catch was used if it was less than 100. Often the weather prevented trawling, or catches were insufficient, at Mercury Bay and The Aldermen Islands. Only the Motiti Island station provided a complete series of samples. To obtain more detailed information on breeding behaviour, a further six visits were made to the Motiti Island grounds between March and June 1969. During this period two stations were worked—one at 180 m, north of Plate Island, and the second at 65 m, between Motiti Island and Plate Island.

During the period April 1967 to July 1968 the data recorded for each fish were fork length (measured to the nearest centimetre below the actual length), sex, gutted weight, and gonad weight; a maturity stage classification was used between February and July 1968. In 1969 fork lengths and sex were recorded, the gonads were staged, and otoliths were collected for age determination. Material was also collected for histological examination of the gonads and for a detailed study of gametogenesis (chapter 5).

Temperature of the water was recorded at most stations with a bathythermograph.

RESULTS

General Observations

The virtual absence of tarakihi smaller than 25 cm in fork length in the Bay of Plenty which had previously been noted (Tong and Elder 1968) was also a feature of the present investigation (Fig. 18). The few small tarakihi taken were all trawled in deep water north of Plate Island in March 1969. The age-frequency distributions and the age-length relationship of the samples collected between March and June 1969 are shown in Figs. 19 and 20 respectively.

Breeding Cycle

The gonadosomatic index, $\frac{\text{gonad weight} \times 100}{\text{gutted body weight}}$, was used to follow changes in the annual cycle of gonad development at the Motiti Island station from April 1967 to July 1968. The monthly means of the gonadosomatic index for males and females are shown in Fig. 21. The monthly sample sizes varied between 10 and 80 for females and 25 and 70 for males. The marked increase in gonad weight in March showed that maturation was a rapid process. The gonadosomatic index remained high during April and May for females, but fell slowly for males during this period. The gonads then remained in a resting condition until the following summer, when there was a very gradual increase in gonad weight. The high standard deviations recorded for the period

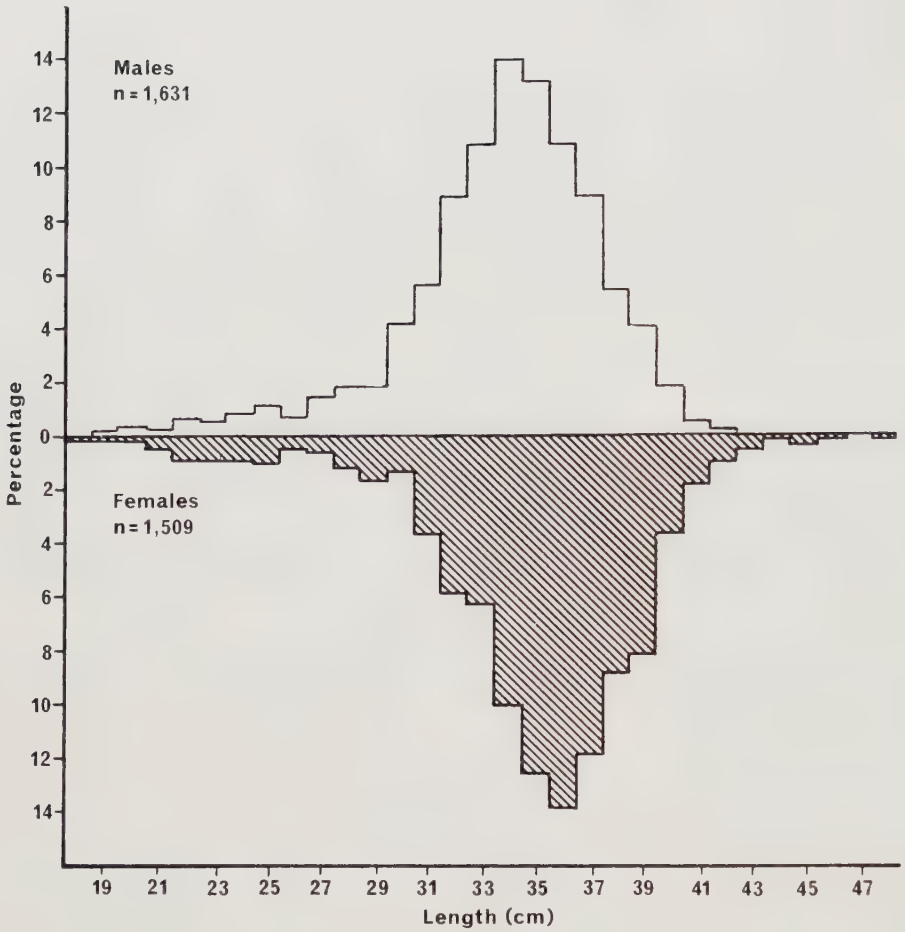


Fig. 18: Length-frequency distributions of the total number of males and females taken in the Bay of Plenty between April 1967 and July 1968 and from March to June 1969.

TABLE 12: Maturity stages for male tarakihi

Stage 0: Virgin. Testes form almost indistinguishable threads in the smaller fish, but are thin and ribbon-like, extending to half length of the body cavity in larger fish. Creamy brown coloration.

Stage 1: Resting mature and recovering spent. Similar to stage 0, but testes thicker and extend to over half length of the body cavity. Darker brown colouring in recovering spents. Stage 1 fish during spawning period are considered immature (see text).

Stage 2: Developing. Testes filling out and colour changing to pink. Firmer texture to lobes, but no milt exudes when they are cut.

Stage 3: Developing. Testes lobes now white, much fatter with scalloped margins. When cut a small amount of milt exudes.

Stage 4: Ripe. Large firm lobes filling body cavity. Milt exudes from genital pore only under pressure.

Stage 5: Running. As for stage 4, but milt exudes freely from genital pore.

Stage 6: Partly spent. Flaccid lobes, looser texture, but large quantities of milt still present.

Stage 7: Spent. Testes completely flaccid, dilated blood vessels, red-brown, some residual sperm.

TABLE 13: Maturity stages for female tarakihi

Stage 0: Virgin. Ovaries consist of very small rounded lobes, no more than 4 cm long for the oldest juveniles. Firm, pale grey-green.

Stage 1: Resting mature and recovering spent. Ovaries similar to stage 0, but about one-third of the length of the body cavity. Stage 1 fish during spawning period are considered immature (see text).

Stage 2: Developing. Ovaries half body cavity length and fatter, pale yellow coloration. Eggs not visible.

Stage 3: Developing. Ovaries over half length of body cavity, yellow coloration, and eggs minute but visible to naked eye.

Stage 4: Maturing. Ovaries large and beginning to fill body cavity. Orange coloration and eggs clearly visible, but no hyaline eggs present.

Stage 5: Ripe. Similar to stage 4, but ovaries filled with hyaline eggs, which are easily expressed. Numerous smaller opaque eggs also present.

Stage 6: Partly spent. Ovaries flaccid, with dilated blood vessels and thickened wall. Both small opaque and hyaline eggs present, but far fewer than in stage 5.

Stage 7: Spent. Ovaries completely flaccid, flattened, and orange-red. Dilated blood vessels and thick ovary wall. Some hard residual eggs are present, which indicates resorption.

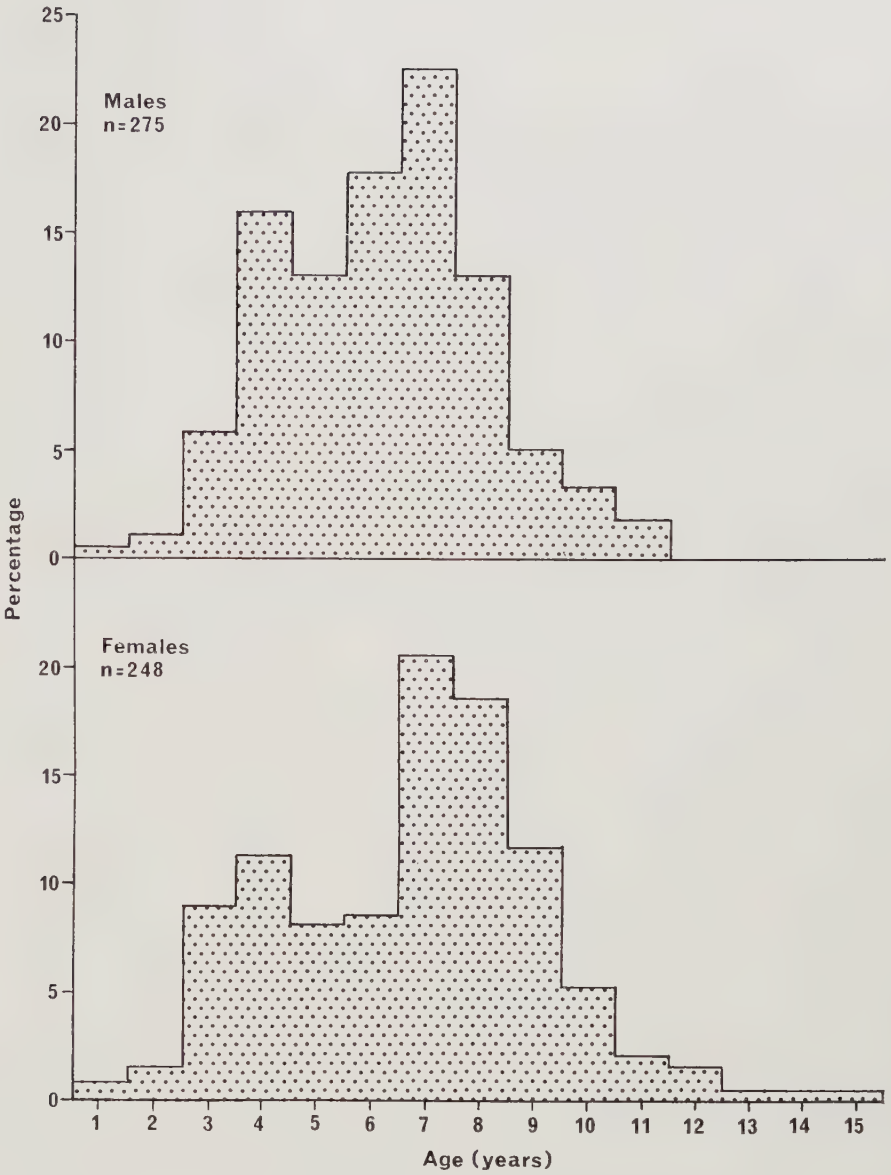


Fig. 19: Age-frequency distributions of males and females taken between March and June 1969.

March to June indicate the great variability in the samples.

Maturity Stage Analysis

To carry out a routine analysis of the maturation cycle for a species of fish, it is essential to have a system of defining stages of gonad development which allows for a rapid assessment of large numbers of fish. Such a system has been used extensively in studies of commercial species, for example, the herring (Iles 1964, Parrish and Saville 1965), by employing criteria such as shape, colour and size of gonads in relation to the size of the body cavity, size of eggs, and freeness of milt. From observations made in 1967 it was obvious that the various stages in tarakihi maturation could be similarly classified. From February 1968 the gonads of tarakihi were staged according to the classification set out in Tables 12 and 13.

In 1968 (Fig. 22) stage 4 males and females were absent in February, but by the end of March they dominated the catches and continued to do so in April. Ripe fish (stage 5) appeared in small numbers in April, but were more numerous in May, with only a few appearing in the June sample. The first partly spent fish (stage 6) appeared in May, and by June almost the whole sample consisted of partly spent and spent fish. In July only spent fish (stage 7) were taken.

The results for 1969 were very similar (Fig. 23)—a gradual appearance of ripe fish during April followed by a decline in May. Again, partly spent

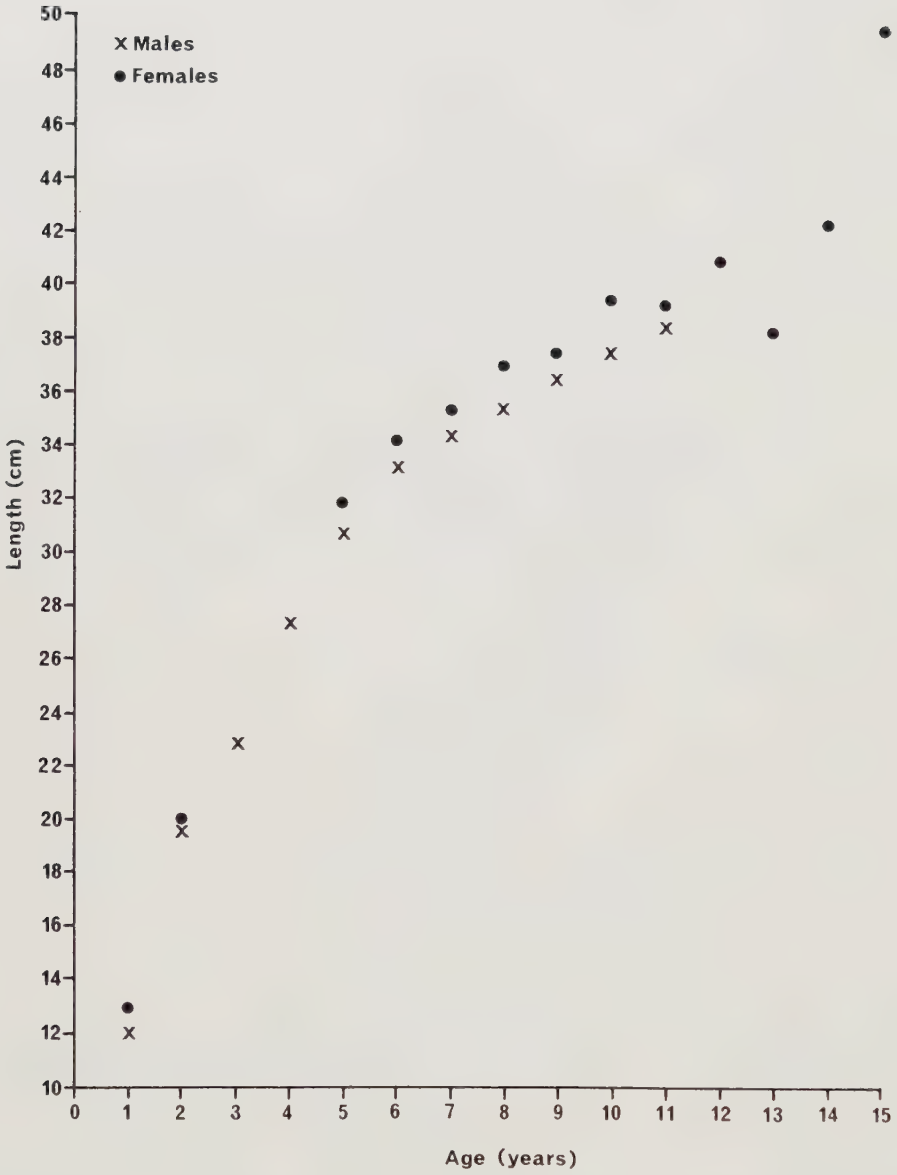


Fig. 20: Average length of each age group for the period March to June 1969.

fish did not predominate until May. Stage 4 fish dominated the catches from March until May, but histological evidence indicated that some stage 4 females had ovulated and spawned (chapter 5). The external appearance of the ovary does not show any indication of this, and, thus, further studies should include supplementary histological observations. Therefore the presence of female stages 4 and 5 in the catches is a true measure of the spawning period, and partly spent fish (stage 6) indicate that the season is nearing its end.

The average length of the fish at each maturity stage has been calculated and the results for the first half of the season in 1968 and 1969 are shown in Tables 14 and 15. The results were similar for both years' observations; the larger fish matured

TABLE 14: Average lengths of each maturity stage for February to April 1968

	Females (cm)					Males (cm)				
	1	2	3	4	5	1	2	3	4	5
February	32.5	35.8	39.3	—	—	31.7	33.8	35.5	—	—
March	28.3	29.0	35.5	36.2	—	—	37*	32.7	34.8	37
April	—	—	32.0	33.0	37.0	—	27.3	32.0	34.7	37.2

* 1 specimen.

A dash indicates that no fish were obtained.

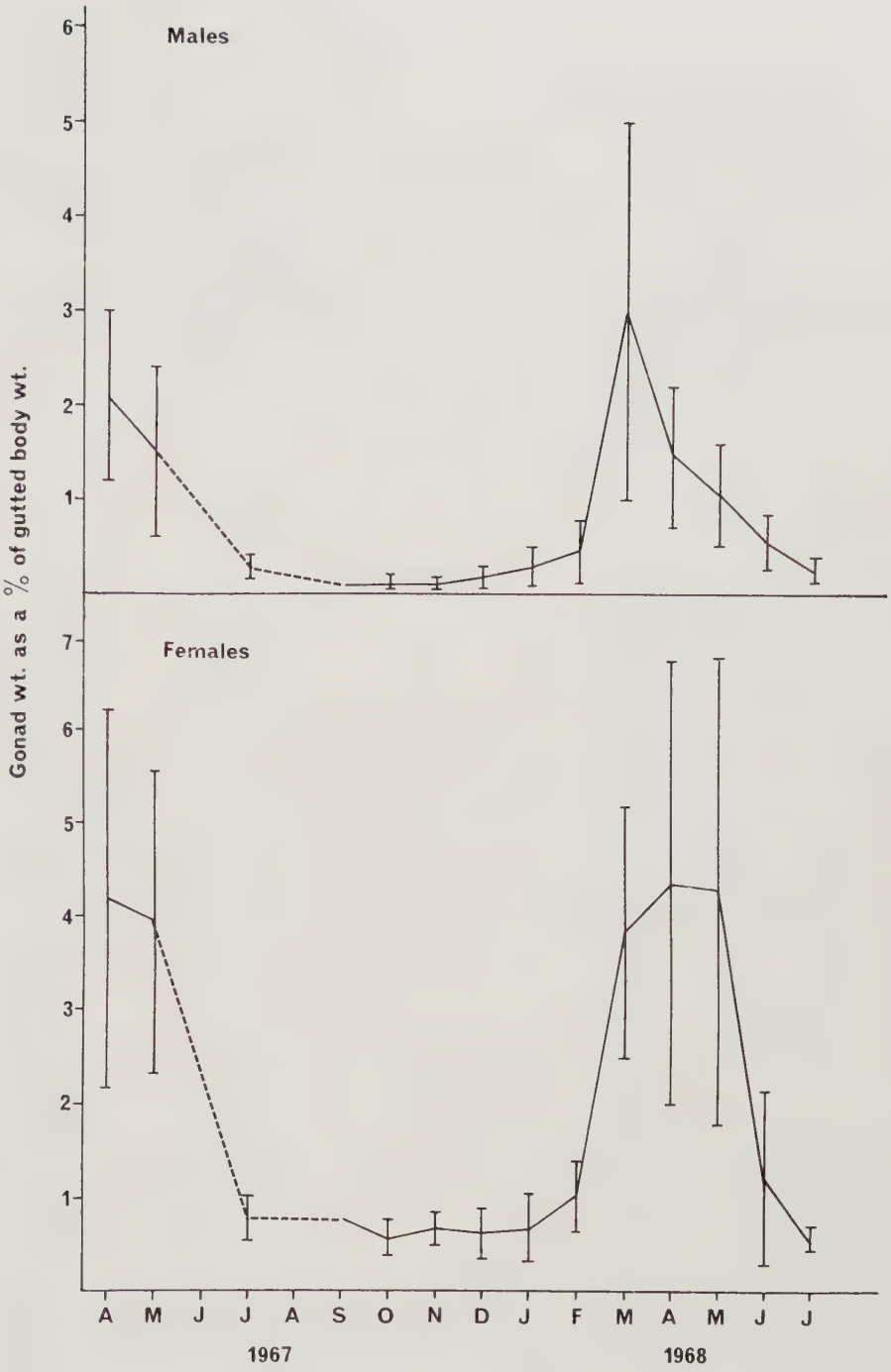


Fig. 21: Gonad weight shown as a percentage of gutted body weight (gonadosomatic index) over the period April 1967 to July 1968. The vertical lines represent one standard deviation about the mean.

TABLE 15: Average length of each maturity stage for March and April 1969

	Females (cm)					Males (cm)				
	1	2	3	4	5	1	2	3	4	5
March	32.8	32.4	35.0	36.9	36.7	29.3	33.3	34.3	36.3	—
1 April	33.0	34.0	33.3	34.9	34	27.0	27.4	30.3	34.0	32.8
9 April	—	—	33.0	36.2	37.1	—	32.0	34.8	33.9	34.3
22 April	—	—	—	35.5	35.8	—	31.0	33.0	33.8	35.0

A dash indicates that no fish were obtained.

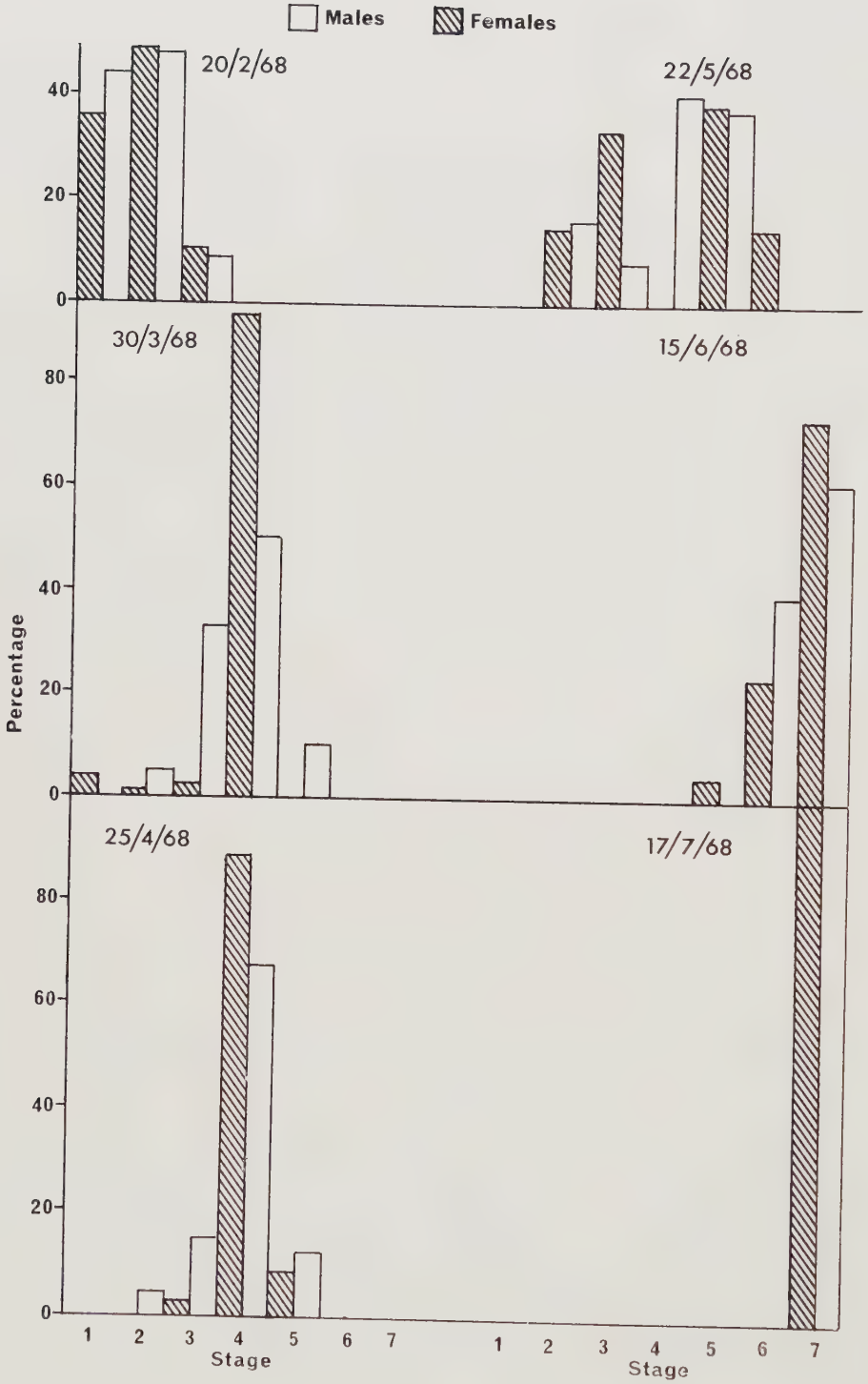


Fig. 22: Analysis of maturity stage frequency for the period February to July 1968.

and ripened earlier than the smaller fish. For this reason the average fish length at each stage decreased as the peak of the spawning period was approached.

Early in 1968, as well as samples from Motiti Island, tarakihi were obtained from Lottin Point, which is between East Cape and Cape Runaway, and Conway Ridge, just south of the Kaikoura Peninsula (Fig. 1). The gonads of these fish were staged and the results showed clear differences between samples from the three areas (Fig. 24). Those fish taken at Conway Ridge in late January were close to spawning, which was clearly demonstrated by a second sample taken 6 days later from

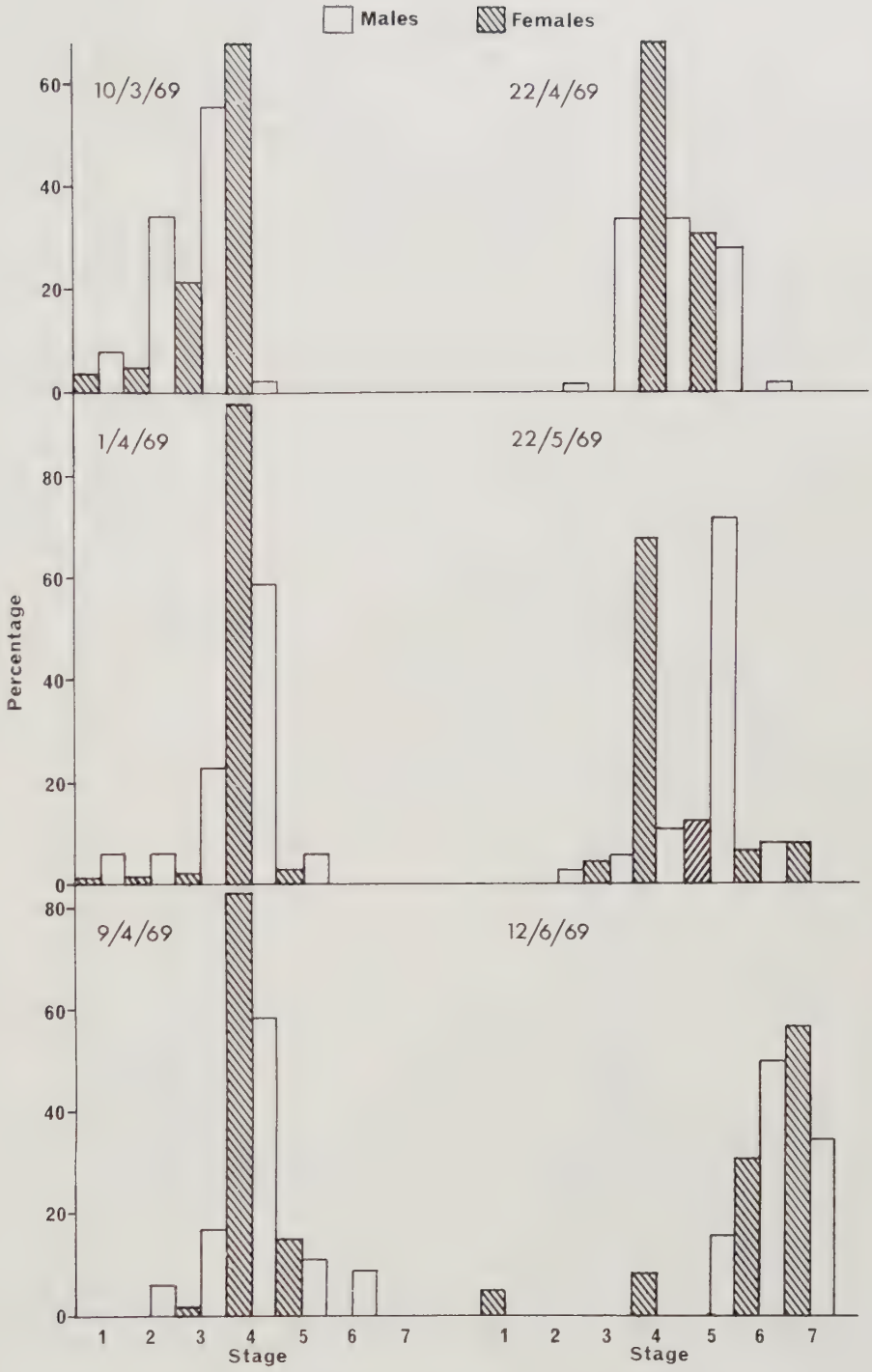


Fig. 23: Analysis of maturity stage frequency for the period March to June 1969.

the same ground; the number of stage 5 fish had increased by over 100 percent. At Lottin Point, toward the end of February, only a few fish were ripe and many fish were still in the early stages of development. At Motiti Island, which was sampled one day before Lottin Point, no fish had reached stage 4 in the maturation cycle, spawning subsequently taking place in April and May.

Age and Length at First Maturity

Tables 16 and 17 show the relationship between age and length at first maturity for tarakihi in the Motiti Island-Plate Island area in the Bay of Plenty for 1969. Otoliths were used to age the fish as described in chapter 2. For classification of maturity both males and females were considered mature when their gonads were at stage 2 or above. Fish

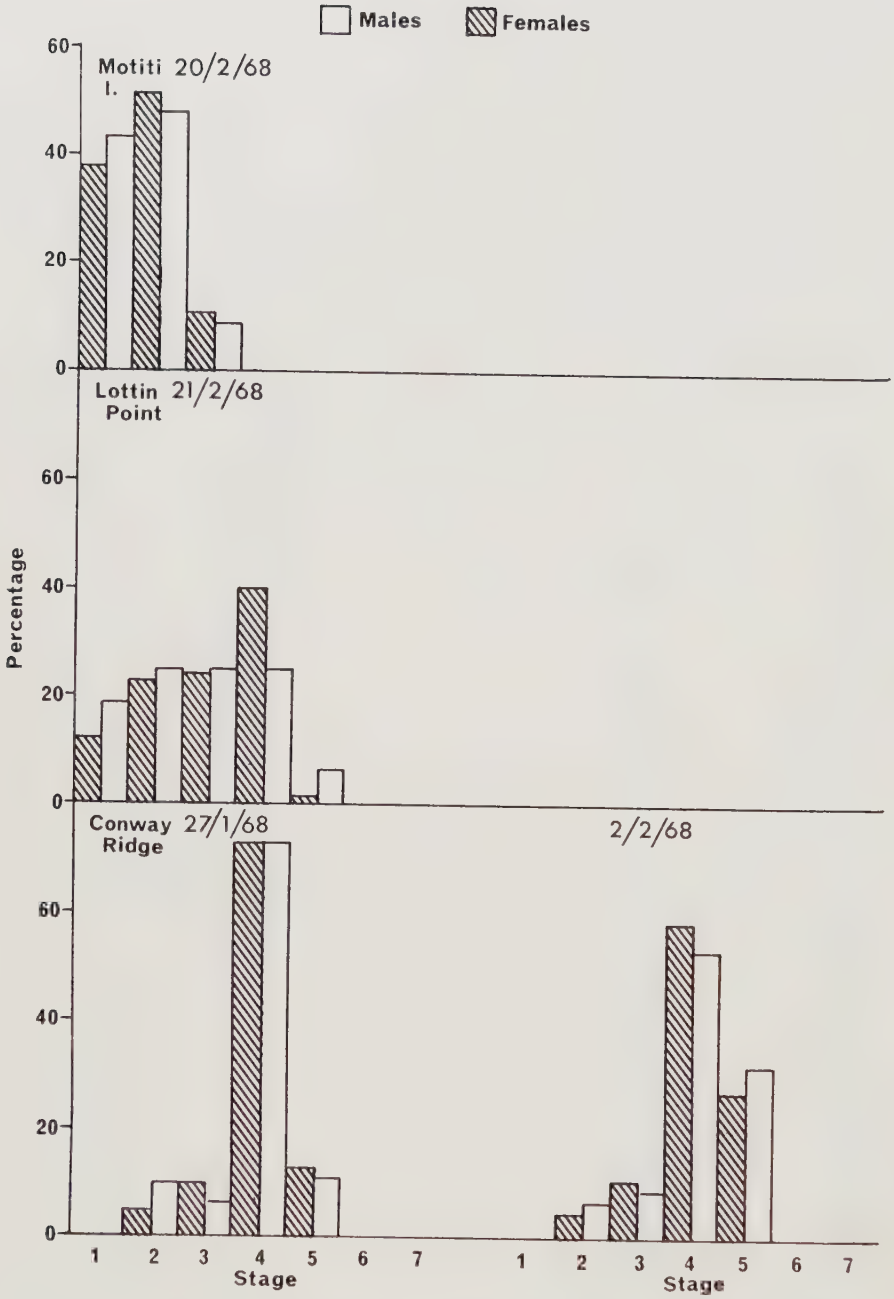


Fig. 24: Analysis of maturity stage frequency for the three areas sampled in January-February 1968.

with stage 1 gonads were classed as immature with the virgins during the spawning season, because further development was unlikely. These fish were always the larger immature specimens and were possibly undergoing some gonad development in their pre-adult year. Outside the spawning season it was not possible to differentiate between stage 1 fish which would remain immature and those which would develop and spawn.

No fish was mature at 3 years, and all fish were mature at 6 years. The higher percentage of mature males in the lower length groups showed that in the 4- and 5-year age groups more males than females were mature. The smallest mature fish was a female of 24 cm, but this was exceptional. All other mature females were greater than 28 cm.

TABLE 16: Percentage mature at each age group

Age (years)	Mature males (%)	Mature females (%)
3	0	0
4	52.3	22
5	93.8	66.6
6	100	100

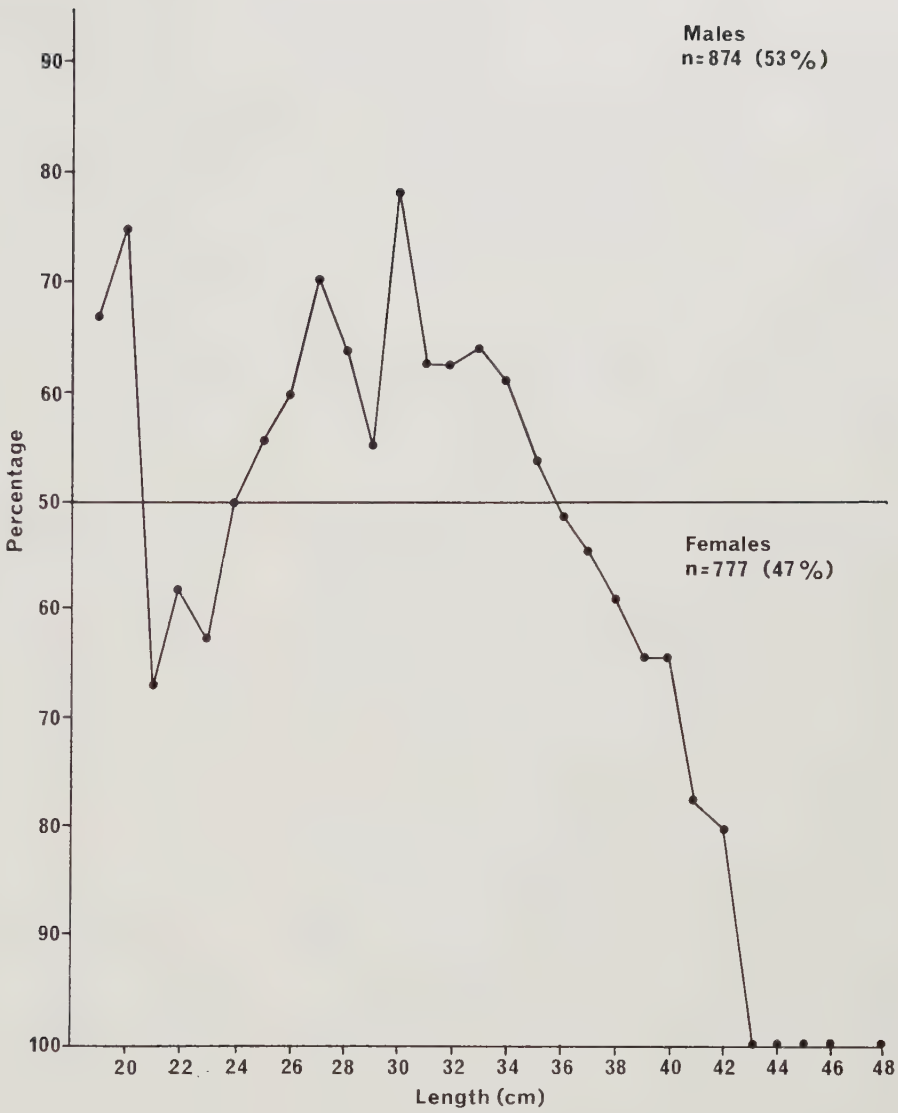


Fig. 25: Sex ratio of each length group for the total catch made between April and July 1967, March and July 1968, and March and June 1969.

Sex Ratio

The sex ratio of all the samples taken in the Bay of Plenty is shown in Table 18. Neither sex completely dominated a catch, but there was a tendency during the spawning period for females to be more numerous in shallower waters, as at Motiti Island in 1969, and for males to be more numerous in deeper waters, as at The Aldermen Islands in 1968 and at Plate Island in 1969.

The total number of tarakihi taken in the Bay of Plenty during the present investigation was 3,140; 53 percent of the catch were males. However, the sex ratio varied with length (Fig. 25). The combined March to July samples for all 3 years showed a sharp increase in the number of males over 24 cm; a return to the 1 : 1 ratio was not reached until the 35-cm group, after which females dominated the catches. A similar pattern was obtained for the period September to February, the resting period of the breeding cycle, but the differences in the sex ratio with size were not so pronounced.

TABLE 17: Percentage mature at each length group

Length (cm)	Mature males (%)	Mature females (%)
23	0	0
24	0	6.7
25	22.2	0
26	14.3	0
27	50	0
28	83.3	50
29	92.3	50
30	91	60
31	100	77.8
32	96	91
33	100	91
34	100	94.1
35	100	100

TABLE 18: Sex ratio of the catches, Bay of Plenty, 1967–69

	Plate I.		Motiti I.		Aldermen Is.		Mercury Bay	
	M	F	M	F	M	F	M	F
1967								
April	—	—	52	48	44	56	28	72
May	—	—	60	40	74	26	—	—
July	—	—	61	39	49	51	—	—
September	—	—	65	35	—	—	54	46
October	—	—	45	55	69	31	44	56
November	—	—	38	62	60	40	52	48
December	—	—	57	43	52	48	47	53
1968								
January	—	—	45	55	—	—	—	—
February	—	—	37	63	71	29	45	55
March	—	—	20	80	92	8	—	—
April	—	—	—	—	79	21	—	—
May	—	—	70	30	83	17	—	—
June	—	—	73	27	—	—	—	—
July	—	—	30	70	52	48	—	—
1969								
March	65	35	20	80	—	—	—	—
April (1)	67	33	16	84	—	—	—	—
April (2)	58	42	15	85	—	—	—	—
April (3)	77	23	—	—	—	—	—	—
May	53	47	14	86	—	—	—	—
June	54	46	15	85	—	—	—	—

A dash indicates that no sample was collected.

DISCUSSION

Weight changes in the gonads of the tarakihi indicate that spawning takes place between March and July on the Motiti Island grounds in the Bay of Plenty. Yamamoto and Yoshioka (1964) considered high ovary weight values over a long period, followed by a gradual decline, typical of teleosts that spawn more than once in a season, and a similar result was obtained for tarakihi. Histological studies have confirmed that tarakihi release more than one batch of gametes in a season (chapter 5), and Han (1964) reported similar results.

With a maturity stage classification it has been possible to understand more fully the annual weight changes in the gonads. The weight gain in both testes and ovaries was very rapid, which was marked by the appearance of large numbers of mature (stage 4) fish in March. Angot's (1951) observations suggested a similar rapid maturation. He recorded moderately developed gonads in the middle of February, but ripe fish were present in the first few days of March.

The peak spawning period for the Motiti Island area was between the middle of April and the middle of May. McKenzie (1961) recorded April for East Cape, Han (1964) recorded March to April in New South Wales waters, and Angot (1951) observed maximum spawning frequency between 7 and 20 March. The present work showed that ripe fish appeared in late February at Lottin Point and that spawning occurred in late January and early February at Conway Ridge. The earliest month recorded for the appearance of ripe tarakihi during summer in New Zealand waters was December, in 1932 (Graham 1939). A summary of all available data on the spawning times of *Cheilodactylus macropterus* is shown in Table 19.

On the east coast of New Zealand spawning appears to take place earlier at higher latitudes (Table 19), and the final maturation and ripening of the gonads is probably related to a drop in sea water temperature. At Motiti Island in 1968 and 1969 ripe tarakihi occurred in the catches when the bottom temperature had fallen from a summer maximum of about 17° C to 16° C in April. Angot's (1951) data also showed spawning to occur on a falling temperature; fish were observed spawning at the surface, the average surface temperature being 15.5° C after having fallen from a January-February maximum of about 17° C. Surface spawning has not been recorded for the species in Australian or New Zealand waters. Since water temperatures fall from their summer maximum earlier in southern New Zealand waters (Skerman 1958), earlier spawning would result in the higher latitudes. This contrasts directly with spring-summer spawners, for example, the whiting, whose spawning occurs later at higher latitudes (Desbrosses 1948) and is related to a rise in temperature (Bowers 1954).

Many male fish attain sexual maturity at an earlier age and smaller size than the females (Hoar 1957), and a similar situation exists for the tarakihi. First maturity occurred at the completion of the fourth year in both sexes. Over 50 percent of males were mature at 4 years, but most females were not mature until completion of the fifth year. Han (1964) reported first maturity to occur at 3 years of age in both sexes in New South Wales. These differences between Australian and New Zealand stocks may be an example of a general phenomenon described by Gunter (1950); animals in colder seas tend to have delayed sexual maturity, slower growth, longer life span, and larger maximum size. A comparison of Han's growth data and those presented here indicates that *C. macropterus* also has a faster growth rate in Australian waters.

A decrease in growth rate occurs at about 5 to 6 years of age, when full maturity is attained (see also chapter 3). After 4 years the growth curves diverge (Fig. 20), females being slightly larger than males for each age group (see chapter 3). This difference may be related to the fact that most males are mature earlier. Many authors have shown similar results for a number of species (see Alm 1959). In addition a very general, though not universal, characteristic of fish is that the female of the species grows

TABLE 19: Summary of available data on the spawning period of *C. macropterus*

Area	Latitude (°)	Authority	Method of assessment	Spawning period	Peak spawning
N.S.W., Australia	34–36	Han 1964	Ripe fish?	February-late April	—
Lottin Point, N.Z.	37–38	McKenzie 1961	Ripe fish and eggs in plankton	April	April
		Present study	Ripe fish	February onward?	—
Motiti I., N.Z.	37–38	Present study	Ripe fish	March to June	Late April to early May
St. Paul I., Indian Ocean	38–39	Angot 1951	Observed spawning fish	March	Mid-March
Conway Ridge, N.Z.	42–43	Present study	Ripe fish	January-February onward?	—
Otago, N.Z.	45–46	Graham 1939	Ripe fish	December	—

larger than the male and also lives longer (Beverton 1964). The shorter life span of the males is often associated with their earlier attainment of sexual maturity (Hoar 1957). During the present investigation the largest and oldest fish were always females, but they were few. Whether this is due to the earlier maturity of the males or whether it is attributable to the fact that males are more active than the females and are thus more vulnerable to fishing operations, as suggested by Alm (1959), is difficult to assess.

The earlier maturity of male tarakihi is reflected in the composition of the catch in relation to length groups, males dominating the catch in the 25- to 34-cm range. With an overall sex ratio of about 1 : 1 it follows that more females than males will be taken in the higher length groups and this occurs once full maturity is attained in the females. Maturity obviously affects the behaviour of the fish. With only a low proportion of sexually immature tarakihi in the samples from commercially fished areas in the Bay of Plenty, it is apparent that tarakihi do not become vulnerable to fishing operations until they are mature.

This very probably happens in all other areas where *C. macropterus* exists, as shown by length-frequency data. In mainland New Zealand waters most records of commercial catches show a typical unimodal length frequency, with fish entering the catches in the range of from 23 to 29 cm (for example, see Waugh 1969) depending on the area fished. At the Chatham Islands trawl catches of tarakihi indicated that fish did not enter the fishery until about 35 cm (our unpublished data), and Angot's (1951) data showed that in the shelf regions around St. Paul Island fish were first taken at 34 cm. In the latter areas the length frequencies were unimodal, with the mode at about 45 cm.

The first fish in the length range probably reflect the approximate length at which fish first mature in that area, with the modal length indicating the length at which full maturity is attained; these lengths would therefore be about 34 cm and 45 cm respectively at both the Chatham Islands and at St. Paul Island. Han's data (1964) support this suggestion, since he reported that the commercial catch in Australian waters "consists of III+ to IX fish, the mode being IV+". First maturity occurred at 3 years, and full maturity probably occurred at 4 years. Length-frequency data therefore appear to reflect both the length at first maturity and the length at which full maturity is attained. The reasons for the differences from area to area remain open, but work at present being carried out in New Zealand waters may resolve this question.

CHAPTER 5

GAMETOGENESIS

By L. J. Tong

INTRODUCTION

The process of gametogenesis in teleosts begins in embryonic life, but continues through active sexual life. Primordial germ cells originate during gastrulation and either migrate or are carried passively by formative processes to the region of the differentiating gonad (Hoar 1957).

In females mitotic division of the germinal epithelium, of follicle cells, or of pre-existing oogonia (Franchi, Mandl, and Zuckerman 1962) results in nests of oogonia, from which the oocytes and mature eggs are formed. Cytological development of the oocyte is basically the same in all teleosts, variations occurring only in the development of the egg membranes.

The teleost testis is composed of cyst-like units in lobular or tubular form. Spermatogenesis is initiated by germ cells, which may migrate into, or are present in, the lobule walls. Mitosis of the germ cells followed by the maturation divisions gives rise to cysts filled with spermatids. The cysts rupture, and fully mature spermatozoa are liberated into the lumina of the lobules.

The previous chapter, in which the reproductive cycle of the tarakihi was described, was restricted to seasonal weight changes in the gonads and to an analysis of the maturity stages. The present chapter, dealing with gametogenesis, completes the preliminary study on the breeding biology.

MATERIAL AND METHODS

Gonads were collected from 10 to 30 tarakihi at about monthly intervals from April 1967 to July 1968 and between March and June 1969. Sampling methods have been described in the previous chapter and all material for the present study came from the Motiti-Plate Islands area (Fig. 1).

Portions of ovaries were fixed in Smith's formol bichromate or sea water Bouin's fluid. Testis segments were fixed in Bouin's fluid. Wax sections, 3 to 10 μm thick, were stained with Heidenhain's haematoxylin, Ehrlich's haematoxylin and eosin, or Hansen's trioxyhaematin.

All measurements were made under a microscope with a moving-hair micrometer.

OBSERVATIONS

Gross Anatomy

The ovaries of the tarakihi consist of two elongated lobes in the dorsal part of the body cavity and underlying the kidneys and swim-bladder. They join at their posterior ends and then form a common oviduct which carries the mature eggs to the exterior via the genital pore. Each ovary, bounded by a wall of muscle containing elastic fibres, is hollow, and its lumen is continuous with that of the oviduct. The internal surface is thrown into numerous folds or lamellae which project into the lumen (Fig. 26) and are lined with a germinal epithelium containing reserve oogonia. In ripe fish the lamellae completely occlude the lumen. Developing oocytes are embedded in a thin stroma of ovarian tissue.

The testes are similarly paired and elongated, but are somewhat flattened. In virgin and resting males the testes are very thin and ribbon-like, extending for over half the length of the body cavity. In maturing fish the testes thicken and have a lobed appearance. The external wall is of very thin muscle containing elastic fibres. Internally, each testis is composed of numerous lobules bounded by connective tissue. Lobules are made up of cysts of germ cells in various stages of maturation, surrounding the lumen, into which the spermatozoa are liberated. The lumina interconnect to form ducts which converge into a main collecting or deferent duct. The two deferent ducts join at the posterior margins of the testes and almost immediately connect with the genital pore.

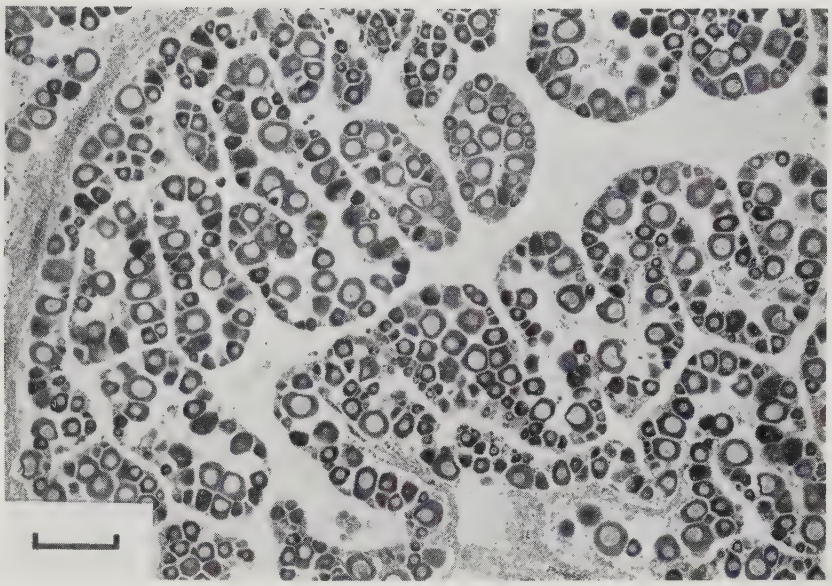


Fig. 26: Transverse section of a resting ovary, showing lamellae and primary oocytes. Scale 200 μm.

Oogenesis

The development of the egg can conveniently be divided into five stages.

Stage 1: Oogonia. These cells are present either singly or in nests around the internal margins of the lamellae in close association with the germinal epithelium (Fig. 27). The average diameter of an oogonium is 10.5 μm, and each cell has a nucleus about 5.5 μm across, with a prominent nucleolus. Oogonia in nests have often passed into the first meiotic division and their normally light-staining basophilic cytoplasm becomes deeper in colour. Potential follicle cells are always associated with nests of oogonia.

Stage 2: Primary Oocyte. The developing eggs of this stage have a size range of from 12 to 100 μm. They have a deep-staining basophilic cytoplasm, but as the cell enlarges it gradually loses its strong affinity for haematoxylin and becomes a grey granular mass (Fig. 26). The nucleus is large and contains, in the smallest oocytes, a single nucleolus, but as growth takes place the nucleoli increase in number and become arranged around the periphery of the nucleus. The chromosomes are loosely arranged; they are in the mid-prophase of the first meiotic division and no further meiotic activity occurs until the egg has completed growth (Richards 1931). A follicular epithelium (the granulosa), one cell thick and surrounding the oocyte, becomes

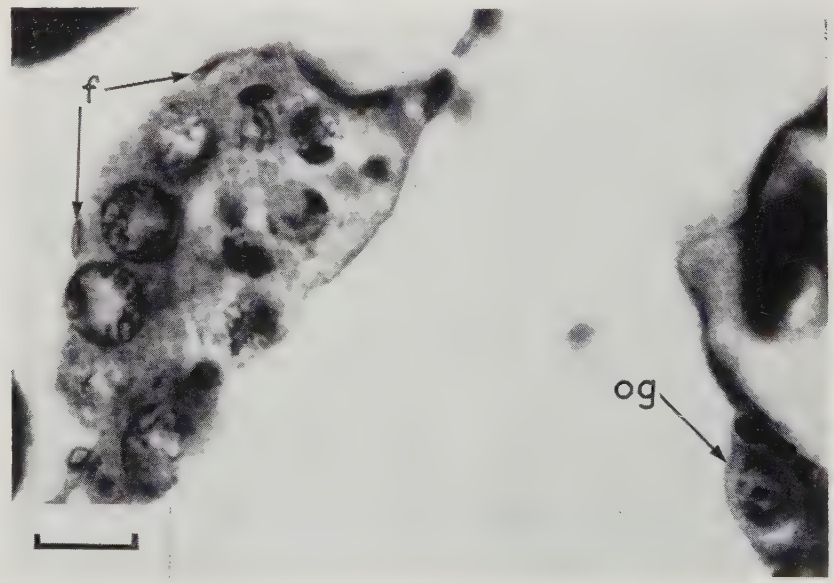


Fig. 27: Transverse section of an ovary, showing a nest of developing oogonia. og — oogonium; f — follicle cells. Scale 10 μm.

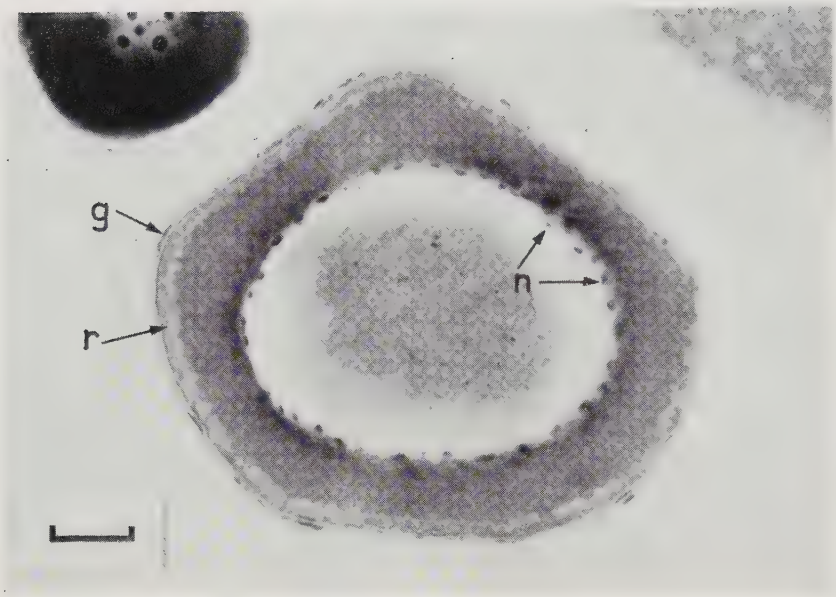


Fig. 28: Fully developed primary oocyte. n — nucleoli; r—zona radiata; g — granulosa. Scale 20 μm.

evident as this stage reaches its maximum size (Fig. 28).

Stage 3: Vacuolation. When the egg is about 100 μm in diameter small vacuoles appear in the cytoplasm (Fig. 28). These enlarge as the egg further increases in size (Fig. 29). During this phase a second membrane forms around the margin of the egg, internal to the follicular epithelium or granulosa. This is the zona radiata, an acellular structure which develops a striated appearance as it thickens (Fig. 30). The nucleus continues to enlarge, but begins to lose its regular, oval outline.

Stage 4: Vitellogenesis (Fig. 29). The first indication of yolk formation is the appearance of small droplets closely associated with the vacuoles in the outer cytoplasm. The droplets, which stain deeply with haematoxylin, enlarge to form spherical globules which rapidly fill the cytoplasm and lead to a rapid enlargement of the egg. During this enlargement the nuclear membrane becomes more irregular in outline and appears to disintegrate. The largest eggs measured in fixed material reached about 500 μm in diameter. The zona radiata averaged 7 μm in thickness. A clear zone of cytoplasm, about 5 μm thick, appears between the zona radiata and the yolk during this stage. This zone is the oolemma (Fig. 30).

The granulosa, consisting of flattened follicle cells, is now stretched around the egg. The cells average 7 μm in length and only 2 to 3 μm in depth. As in most teleosts the theca is barely visible, consisting

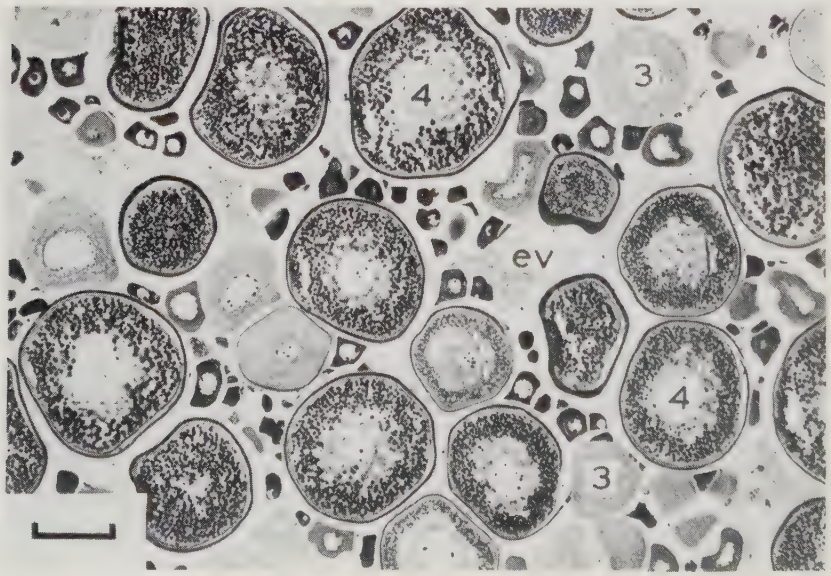


Fig. 29: Transverse section of a mature ovary, showing various stages in egg development. 3 — vacuolation; 4 — vitellogenesis; ev — evacuated follicle. Scale 200 μm.

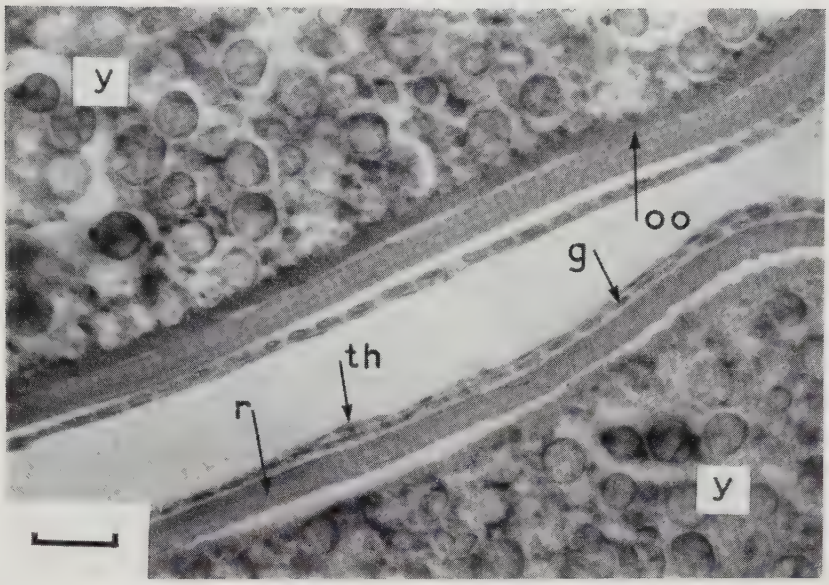


Fig. 30: Detail of egg. th — thecal cell; g — granulosa; r — zona radiata; y — yolk globules; oo — oolemma. Scale 20 μm.

of a connective tissue hymen containing the occasional flattened nucleus (Fig. 30).

Stage 5: Mature Eggs. Some ovaries fixed in Gilson's fluid for subsequent fecundity studies contained ripe eggs, which were easily identified by the presence of an outer clear membrane. The average diameter of a ripe egg was 0.93 mm.

Non-gametic Components of the Ovary

The ripe egg is released into the lumen by rupture of the follicular membrane and lamella wall. The granulosa and theca remain, fold and collapse, and fill the space previously occupied by the egg (Fig. 31). Both the theca and granulosa change greatly. The granulosa cells enlarge, their nuclei becoming rounded and strongly basophilic. The theca cells enlarge similarly, but become very irregularly shaped. Erythrocytes become closely associated with the thecal tissue. The mass of cells then diminishes in size and disappears, leaving no trace.

Eggs are resorbed both before and after spawning and form corpora atretica. Their formation differs slightly in the different sized eggs, but the final structure is identical.

Atresia or resorption occurs only in eggs which are in, or have passed, the vacuolated stage (Fig. 32). It begins with a change in the appearance of the cytoplasm and yolk globules; the former becomes granular and the latter liquefy. The radiata loses

Fig. 31: Evacuated follicles. th — theca; g — granulosa. Scale 30 μm.

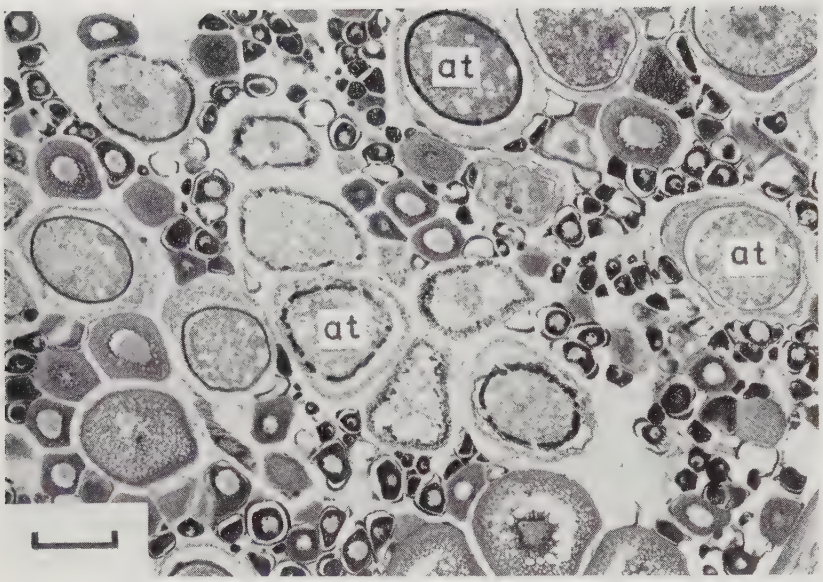


Fig. 32: Transverse section of an ovary, showing numerous resorbing eggs (at). Scale 200 μm.

its regular structure and ruptures in several places. The granulosa cells and nuclei enlarge considerably, but the theca remains unchanged.

The granulosa cells invade the egg, ingesting the debris; there is no enlargement over the initial size of the egg. Large vacuoles appear and erythrocytes become associated with the phagocytosing granulosa cells (Fig. 33). The latter diminish in number and gradually the whole structure shrinks, forming a ball of cells containing a yellow pigment. These corpora atretica, the final form of which is often referred to as a "yellow body", are present throughout the year, but only in small numbers (Table 20). Most post-ovulatory corpora atretica reach the vacuolated stage and then remain unchanged until September or October, when the final degeneration results in the forming of "yellow bodies", which either disappear or remain until January.

RESULTS

A quantitative measure of oogenesis was obtained by use of the staging technique for egg development described above. The number of oogonia, oocytes, developing oocytes, corpora atretica, and evacuated follicles along two to four lamellae were counted, from histological sections, and the occurrence of each stage was expressed as a percentage of the total. The results from all ovaries collected have been combined to show the changes over an 11-month period (Table 20) and for the various stages in the maturation cycle described in chapter 4 (Table 21). Since many ovaries in March 1968 contained a high

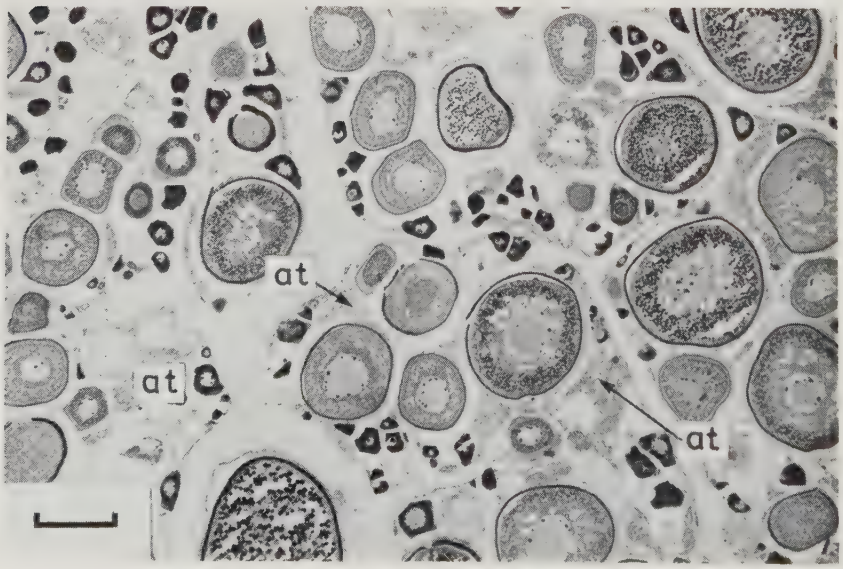


Fig. 33: Transverse section of an ovary of a returned tagged fish, showing late stages in resorption and normal development. at — atretic eggs. Scale 200 μm.

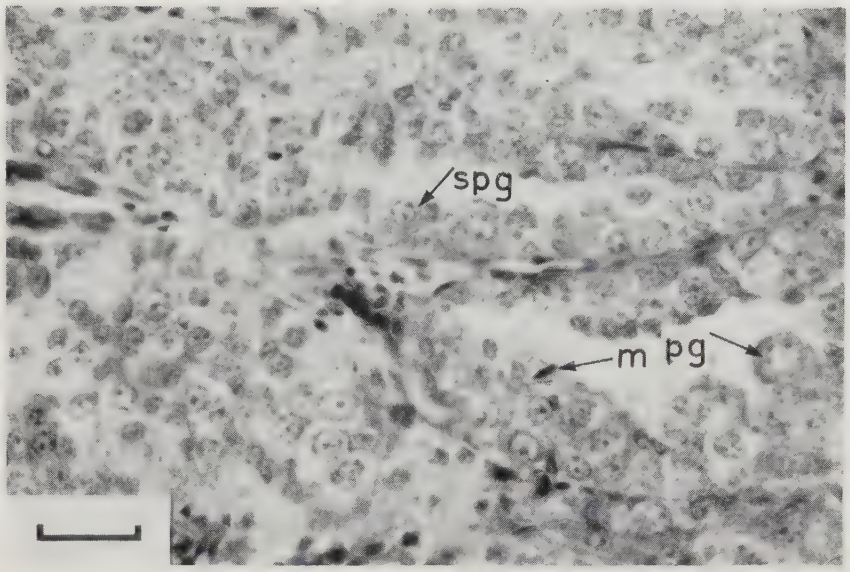


Fig. 34: Transverse section of a testis, showing early stage in spermatogenesis. m — mitotic figure; pg — primary germ cell; spg — spermatogonia. Scale 20 μm.

percentage of corpora atretica, these results appear as a separate item in Table 21 and are excluded from the data in Table 20.

Oogonial proliferation appeared to be at a maximum in September, though no mitotic divisions were observed. Oogonial numbers were also high in July. Table 21 shows that proliferation was probably at its greatest in spent fish, that is, stage 7 in the maturity stage analysis (chapter 4). In one recently spent fish 35.7 percent of the total eggs counted were oogonia. Mitotic figures were observed only in two ovaries and in both instances the fish were recently spent.

There was always a reserve of primary oocytes, the lowest percentage recorded being 58 for ripe (stage 5) ovaries. The average for any month did not fall below 67 percent. A few vacuolated oocytes first appeared in January, but yolk formation, which was reflected in a rapid increase in ovary weight (Fig. 21), did not begin until March. Premature yolk development, which was observed in a few oocytes in January and February, had been arrested by resorption, but corpora atretica did not normally appear in significant numbers until May, when the first spent fish were taken. "Yellow bodies", formed from the previous year's unspawned eggs, were present until the new maturation cycle began.

TABLE 20: Average percentage frequency of the various stages in oogenesis over an 11-month cycle

	Oogonia	Primary oocytes	Vacuol-ation	Vitello-genesis	Atretic	Evac. foll.
September	23.0	74.3	0	0	2.7	0
October	18.6	80.7	0	0	0.7	0
November	17.4	82.1	0	0	0.5	0
December	12.5	86.6	0	0	0.9	0
January	12.7	79.3	8.1	0	0.9	0
February	13.4	78.9	5.9	0	1.8	0
March*	3.3	67.3	15.2	14.0	0.3	0
April	9.5	68.9	16.7	2.9	2.1	0
May	14.0	67.5	6.7	5.1	4.9	1.8
June	14.4	75.4	0.7	1.0	8.0	0.5
July	17.4	78.3	0	0	4.2	0

* Excluding March 1968.

SPERMATOGENESIS

Primary germ cells are present in the testes throughout the year—during the maturing phase as isolated cells in the thin connective tissue sheath surrounding each lobule (Fig. 34) and during the resting phase as a single layer of cells surrounding each lumen. Their cell diameter averages 9.5 μm and the nucleus 5 μm. Mitosis appears to begin in July in spent males, since a few groups of small cells, the spermatogonia, are present. By September mitosis is well advanced, the whole testis being filled with actively dividing primary germ cells and spermatogonia (Fig. 34). This activity results in the formation of nests or cysts of spermatogonia, which have an average nuclear diameter of 3.7 μm. Mitotic divisions continue to appear until February, but the main period of multiplication takes place in spring.

TABLE 21: Average percentage frequency of the various stages in oogenesis for each stage in the maturation cycle

	Oogonia	Primary oocytes	Vacuol-ation	Vitello-genesis	Atretic	Evac. foll.
Stage 2	13.4	79.3	6.6	0	0.6	0
Stage 3	13.3	71.0	14.5	0	1.2	0
Stage 4 March 1968	4.7	69.0	17.8	3.1	5.4	0
Stage 4 March 1969	3.0	62.0	17.0	17.4	0.6	0
Stage 5	1.6	58.1	22.5	17.1	0.8	0
Stage 6	5.4	75.7	7.2	5.5	4.4	1.8
Stage 7	26.1	67.2	0	0	6.7	0

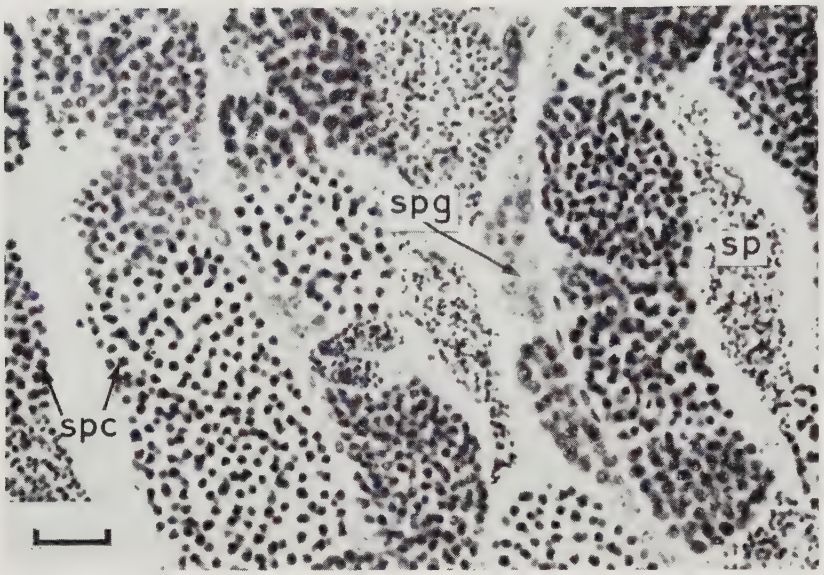


Fig. 35: Transverse section of a testis, showing the various stages in sperm formation. spg — spermatogonia; spc — spermatocytes; sp — spermatozoa. Scale 30 μm.

The first reduction divisions occur in October, and in November numerous cysts of meiotically dividing cells appear in the testis (Fig. 35). Each cyst contains cells at the same stage of development; in November they are mainly primary and secondary spermatocytes, with the occasional nest of spermatids. Nuclear diameter decreases considerably, the average being 2.2 μm for primary spermatocytes, 1.6 μm for secondary spermatocytes, and 1.2 μm for spermatids.

Spermatogenesis is well advanced in December and sperm formation has begun in most fish. Spermatozoa first appear in small numbers in the lumina, but not in the main collecting ducts. Spermatogenesis and spermiation continue through to April, with nests of spermatogonia becoming few, spermatocytes, spermatids, and spermatozoa increasing, and the lumina, ducts, and main collecting ducts gradually filling with mature sperms. In a fully ripe male the testis is composed of spermatozoa-filled lobules, bounded by a thin stretched connective tissue sheath containing isolated cells and the occasional primary germ cells (Fig. 36).

In partially spent males the connective tissue increases in amount and content and the primary germ cells are already beginning to form a single layer around the collapsed lobules (Fig. 37). Fully spent males have a similar appearance, but only a few residual spermatozoa are present.

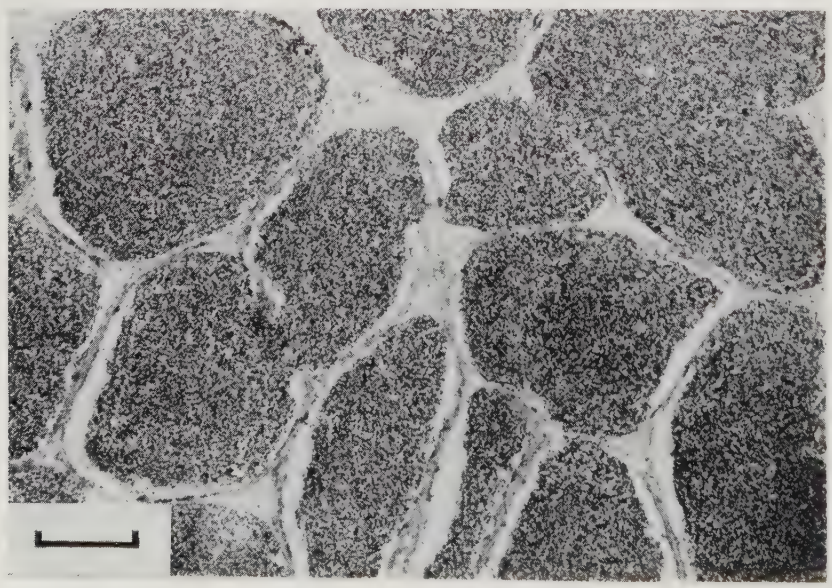


Fig. 36: Transverse section of a mature testis, showing lobules filled with sperm. Scale 100 μm.

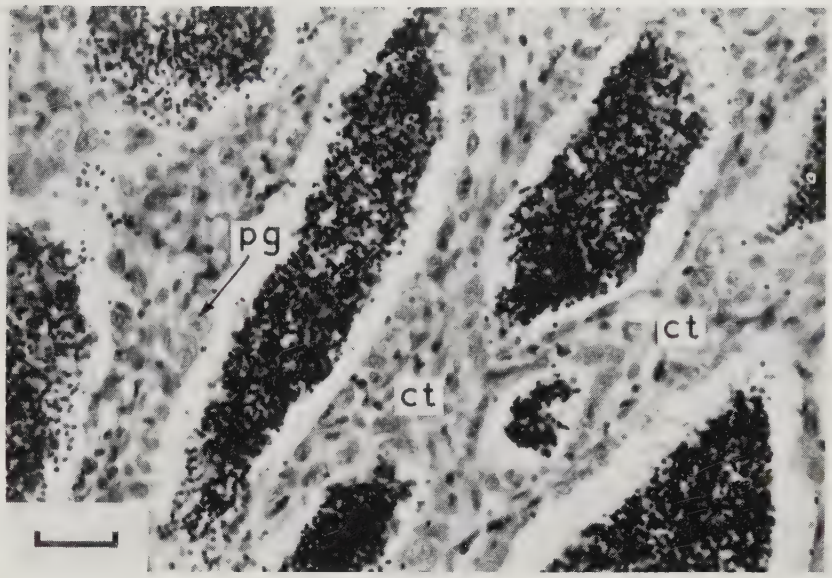


Fig. 37: Transverse section of a semi-spent testis. pg — primary germ cell; ct — connective tissue. Scale 20 μm.

CORRELATION OF MICROSCOPIC CHANGES WITH THE MATURITY STAGE INDEX

In Tables 22 and 23 a brief description of the histological appearance of the gonads is matched with each of the eight maturity stages, full details of which are presented in chapter 4.

DISCUSSION

Gametogenesis in the tarakihi is very similar to that described for most teleosts. Spermatogenesis is initiated by mitotic division of germ cells with the formation of cysts of spermatogonia. Reduction division results in spermiation. Sperms are produced as early as stage 2 in the maturation cycle; subsequent phases result only in increased production of sperm, with running ripe males appearing in April in the Motiti and Plate Islands area (Figs. 22 and 23). Partially spent males are found as late as July.

Oocytes are formed from pre-existing oogonia by mitotic division, which has been observed in only recently spent females. However, mitosis is a rapid process and easily missed (Barr 1963a) and thus multiplication could continue from July until November, when relatively high percentages of oogonia are recorded. The occurrence of large numbers of oogonia undergoing the first meiotic prophase during the latter period, particularly in spring, strongly suggests that there is a renewal of oocytes during this phase of the reproductive cycle.

TABLE 22: Histological description of each maturity stage in males

Stage	Classification	Histological description
0	Virgin	Primary germ cells.
1	Resting	Primary germ cells, spermatogonia, mitosis.
2	Developing	All stages, sperm in lumen only, some mitosis.
3	Developing	All stages, occasional mitosis, sperm extend into collecting ducts.
4	Ripe	All stages, few spermatogonia, no mitosis, collecting ducts filled with sperm.
5	Running	Sperm only, plus isolated primary germ cells.
6	Partly spent	Partial collapse of lobules, but abundant sperm still present, erythrocytes invading tissue.
7	Spent	Complete collapse of lobules, residual sperm only, massive connective tissue increase.

TABLE 23: Histological description of each maturity stage in females

Stage	Classification	Histological description
0	Virgin	Oogonia and primary oocytes only.
1	Resting	Oogonia and primary oocytes only.
2	Developing	Oogonia, oocytes, and isolated vacuolated oocytes.
3	Developing	Oogonia, oocytes. Vacuolated oocytes and small yolked eggs numerous.
4	Maturing	All stages, several groups of eggs, some fully yolked and ready for ovulation, others less yolked, others vacuolated only. In some ovaries evacuated follicles are also present, which indicates a partially spawned fish.
5	Ripe	As stage 4, but ovulated ripe hyaline eggs in the lumen, and evacuated follicles numerous.
6	Partly spent	Evacuated follicles present and some resorption of unspawned eggs.
7	Fully spent	Reserve oocytes, resorbing unovulated eggs, mitotic proliferation of oogonia.

Apart from vacuolation of a few oocytes, further growth of the eggs does not take place until February-March. This development is asynchronous, and between March and June the ovaries contain eggs at all stages of development (Table 20). Asynchronous development is considered typical of fish that spawn more than once in a season (Yamamoto and Yoshioka 1964). Many primary oocytes do not develop, but remain in a resting state throughout the maturation cycle. These resting oocytes always outnumber the maturing ones; they remain after spawning and probably provide the following year's maturing oocytes (Hickling 1930, Yamamoto 1956, Bowers and Holliday 1961).

The eggs are not all ovulated and spawned together. Partially spawned fish were taken during the spawning season, sectioned material containing evacuated follicles. The presence of evacuated follicles in teleost ovaries is certain evidence that the fish have recently spawned (Yamamoto and Yoshioka 1964), and the presence of additional yolked eggs strongly suggests the possibility of further spawnings. However, the number of spawnings, the number of eggs spawning, and the interval between spawnings cannot be determined from sectioned ovaries alone. Few empty follicles were observed and they appeared to have been recently formed. In the medaka, *Oryzias latipes*, empty follicles disappeared in about 3 days (Yamamoto and Yoshioka 1964), and similar results were obtained for the dab, *Pleuronectes limanda* (Wheeler 1924), and a flounder, *Liopsetta obscura* (Yamamoto 1956). Thus the tarakihi follicles probably also disappeared rapidly.

Resorption of eggs, which results in the formation of corpora atretica, has been observed in many teleosts (Pickford and Atz 1957, Beach 1959, Barr 1963a, Rastogi 1966). The dependence of the developing egg on the pituitary hormones has been well established (Pickford and Atz 1957, Ball 1960, Barr 1963b, Yamazaki 1965), but Barr (1963a) suggested that the small number of corpora atretica found in the maturing ovary of the plaice may be accounted for by the mechanical failure of the follicle to provide sufficient nourishment for the developing egg. Similarly, this may account for the small number of pre-ovulatory corpora atretica found in most tarakihi ovaries.

However, as Faleeva (1965) pointed out, not only is atresia a widespread phenomenon in fish, it is also one of the earliest signs of a disturbance in spawning conditions. Such a disturbance may have caused the high degree of resorption in tarakihi ovaries in March 1968. The 5.4 percent resorption recorded for stage 4 females in fact represented over 20 percent of the developing eggs. Scott (1962) showed that the degree of follicular atresia in *Salmo gairdneri* was associated with the degree of starvation, and, similarly, Hodder (1965) suggested that severe food restrictions may induce resorption of ova. June (1970) concluded that the high incidence of atresia in ovaries of northern fishes probably resulted from interruptions of spawning associated with fluctuations in water temperature or level. Although high resorption rates obviously occur in teleosts, Faleeva (1965) considers that atresia is an important adaptation when breeding conditions are disturbed and that this reaction by the fishes does not hinder the development of the young generation of oocytes and subsequent breeding within the same spawning season. Whether this applies to tarakihi, and particularly to those sampled at Motiti Island in March 1968, is difficult to assess.

Evidence from the ovaries of one tarakihi supports Faleeva's conclusions. A tagged tarakihi returned in March 1970, 3 months after its release, had moderately developed gonads, the number of ripening eggs being fairly small. A section of the ovary is shown in Fig. 33. Massive resorption had taken place well before recapture, possibly after tagging, but normal development had continued in some ova. Since no other fish were taken, the extent of resorption in the population could not be observed, but this specimen did indicate that normal development can continue after massive resorption.

Post-ovulatory corpora atretica also registered a high percentage in some spent tarakihi, the average for stage 7 being 6.7, which would account for a large number of the oocytes which were potentially ripe eggs at the beginning of the spawning period. Yamamoto and Yamazaki (1961) considered that the presence of large numbers of atretic eggs in the spent ovary was a further characteristic feature of fish with asynchronous development of the eggs and multiple spawnings. In the last phase of spawning of the goldfish these authors had difficulty in deciding whether the groups of oocytes laden with yolk would proceed to spawning or degeneration. The same observation applies to the current studies on tarakihi.

Two points that must be considered at this stage are the effects of resorption on fecundity and on the estimation of fecundity. Scott (1962) observed that atresia resulted in lowered fecundity, and Hodder (1965) considered a similar relationship existed in the haddock in 1959. June (1970) also linked a high incidence of atresia with a low year class abundance. Even if teleosts can recover from high resorption as Faleeva (1965) suggests, the overall fecundity in a season must be affected. Estimates of fecundity would also be subject to gross

errors, particularly when there is no way of determining the amount of resorption of unspawned eggs. Histological observations would therefore be essential in any fecundity study on fish that experience resorption. In addition, fecundity could be determined at different stages in the maturation cycle as was carried out on the herring (Baxter 1963). Histological observations would also be necessary to determine the minimum size of egg to be counted, since, with asynchronous development and probable multiple spawnings, counts of only ripe eggs would give falsely low estimates.

It is obvious from this study that histological observations alone are not sufficient to determine the exact nature and time of spawning. Before releasing their eggs the fish may remain for a long time in a pre-spawning condition. However, tarakihi have been collected with developing ripe eggs and with evacuated follicles, which suggests that spawning takes place more than once in each individual in each season, and Han (1964) reported similar conclusions for the fish in Australian waters. At present it is not possible to suggest the frequency of the successive spawnings, though it does appear that there is a prolonged spawning season. The only reliable method for assessing the onset and duration of the spawning season will be by sampling the planktonic eggs.

SUMMARY

Although the tarakihi, *Cheilodactylus macropterus* (Bloch and Schneider), is the second most important wet fish landed in New Zealand, little is known about its biology. Between 1967 and 1969 a study was carried out in the Bay of Plenty to obtain basic biological information on age determination, growth, and breeding biology as a preliminary to studies on the New Zealand tarakihi fishery.

The saccular otolith of the tarakihi has a regular pattern of opaque and hyaline zones. Analysis of the seasonal changes in the pattern at the edge of the otoliths and a comparison of otolith zone counts with length-frequency distributions of fish samples show that two major zones are formed annually—an opaque zone in spring-summer and a hyaline zone in autumn-winter. The general pattern is the same throughout the life of the fish, with the exception of the first winter, when no hyaline zone is formed. Two experienced observers, reading otolith samples independently, reached agreements of interpretation ranging from 72 to 93 percent, which indicates that objective criteria for interpreting the otoliths can be defined. The tarakihi otolith is therefore a satisfactory medium for age determination and provides one of the basic requirements for further study of the population dynamics of the species.

Fish of 3 to 9 years old dominated most catches, and age groups 0 to 2 were virtually absent. Annual growth took place in two periods, September to January and April to May, and was separated by a short period of cessation of growth coinciding with the spawning season. From age 6 years onward, the annual growth rate was higher in the females than in the males. There were no differences in growth rate between sampling stations. Growth rate decreased after age 5 years. A von Bertalanffy growth equation was fitted: $L_\infty = 39.9$ cm, $K = 0.26$, $t_0 = -0.49$ year. These values differ from those found in the East Cape area, where growth rate after age 6 years is much higher. Equations expressing the length-weight relationship were determined for all sampling months. For a given fish length weight increased in summer and decreased in late autumn, but the magnitude of this fluctuation was small.

Weight changes in the gonads of the tarakihi indicate a rapid maturation, a long spawning season, and multiple spawning. A maturity stage classification is described and results from its use are presented. The spawning season in the Bay of Plenty extends from March to June, with peak spawning occurring in April and May. Larger fish mature earlier and there is a gradual appearance of ripe fish during April. The peak spawning period varies in New Zealand waters, fish in more northern latitudes generally spawning later in the season. Temperature may be an influencing factor. Males mature at an earlier age and smaller size than females. Fish do not normally become vulnerable to fishing operations until they are mature.

Microscopic examination of the gonads has shown that the macroscopic classification of the maturation cycle corresponds to definite phases of development. Egg development is asynchronous, and spawning probably occurs more than once per season in an individual. The formation of corpora atretica is described and the effect of resorption on fecundity is discussed.

ACKNOWLEDGMENTS

The authors thank the staff of the Ministry of Agriculture and Fisheries fishery research vessels, *Ikatere*, *James Cook*, and *W. J. Scott*, and the master and crew of the trawler *Kotuku*, Nelson, for their assistance in collecting fish samples. Our thanks also go to our colleagues in the Fisheries Research Division, Wellington, for their assistance and for their criticism and suggestions during the preparation of this bulletin.

REFERENCES

ALM, G. 1959: Connection between maturity, size, and age in fishes. *Rep. Inst. Freshwat. Res. Drottningholm 40*: 1–145.

ANGOT, M. 1951: Observations sur la faune marine et la pêche aux îles Saint-Paul et Amsterdam. *Mém. Inst. scient. Madagascar 6*: 1–51.

ARKIN, H., and COLTON, R. R. 1964: "Tables for Statisticians." 2nd ed. Barnes and Noble, New York. 168 pp.

BALL, J. N. 1960: Reproduction in female bony fishes. *Symp. zool. Soc. Lond. 1*: 105–35.

BARR, W. A. 1963a: The endocrine control of the sexual cycle in the plaice, *Pleuronectes platessa* (L.). I. Cyclical changes in the normal ovary. *Gen. compar. Endocr. 3*: 197–204.

——— 1963b: The endocrine control of the sexual cycle in the plaice, *Pleuronectes platessa* (L.). II. The endocrine control of oogenesis. *Gen. compar. Endocr. 3*: 205–15.

BAXTER, I. G. 1963: A comparison of fecundities of early and late maturity stages of herring in the north-western North Sea. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer 154*: 170–4.

BEACH, A. W. 1959: Seasonal changes in the cytology of the ovary and of the pituitary gland of the goldfish. *Can. J. Zool. 37*: 615–25.

BERG, C. 1895: Enumeración sistemática y sinonimíca de los peces de las costas Argentina y Uruguaya. *An. Mus. nac. B. Aires 4 (Ser. 2, 1)*: 1–120.

BEVERTON, R. J. H. 1964: Differential catchability of male and female plaice in the North Sea and its effect on estimates of stock abundance. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer 155*: 103–12.

BEVERTON, R. J. H., and HOLT, S. J. 1957: On the dynamics of exploited fish populations. *Fishery Invest., Lond., Ser. 2, 19*. 533 pp.

BLACKER, R. W. 1969: Chemical composition of the zones in cod (*Gadus morhua* L.) otoliths. *J. Cons. perm. int. Explor. Mer 33*: 107–8.

BLOCH, M. E., and SCHNEIDER, J. G. 1801: "Systema Ichthyologiae", Vol. 55, pp. 336–45. Schneider, Berlin.

BOWERS, A. B. 1954: Breeding and growth of whiting (*Gadus merlangus* L.) in Isle of Man waters. *J. mar. biol. Ass. U.K. 33*: 97–122.

BOWERS, A. B., and HOLLIDAY, F. G. T. 1961: Histological changes in the gonad associated with the reproductive cycle of the herring (*Clupea harengus* L.). *Mar. Res. 5*. 16 pp.

CRAGG-HINE, D., and JONES, J. W. 1969: The growth of dace *Leuciscus leuciscus* (L.), roach *Rutilus rutilus* (L.) and chub *Squalius cephalus* (L.) in Willow Brook, Northamptonshire. *J. Fish Biol. 1*: 59–82.

CUVIER, G. L. C. F. D., and VALENCIENNES, A. 1830: "Histoire Naturelle des Poissons", Vol. 5, pp. 362–5. Levrault, Paris.

DANNEVIG, E. H. 1956: Chemical composition of the zones in cod otoliths. *J. cons. perm. int. Explor. Mer 21*: 156–9.

DEGENS, E. T., DEUSER, W. G., and HAEDRICH, R. L. 1969: Molecular structure and composition of fish otoliths. *Mar. Biol. 2*: 105–13.

DESBROSSES, P. 1948: Le merlan (*Gadus merlangus* L.) de la côte française de l'Atlantique (deuxième partie). *Revue Trav. Off. (scient. tech.) Pêch. marit. 14*: 71–104.

DEVINCENZI, G. J. 1924: Peces del Uruguay. II. Nuestra fauna ictiológica según nuestras colecciones. *An. Mus. nac. Montevideo Ser. 2, 5*: 139–283.

EINARSSON, H. 1951: Racial analyses of Icelandic herrings by means of the otoliths. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer 128 (1)*: 55–74.

FALEEVA, T. I. 1965: Analysis of ovocyte atresia in fish in connection with adaptive role of this phenomenon. *Vop. Ikhtiol. 5 (3(36))*: 455–70.

FORD, E. 1933: An account of the herring investigations conducted at Plymouth during the years from 1924 to 1933. *J. mar. biol. Ass. U.K. 19*: 305–84.

FRANCHI, L. L., MANDL, A. M., and ZUCKERMAN, S. 1962: The development of the ovary and the process of oogenesis. *In* Zuckerman, S. (Ed.), "The Ovary", Vol. 1, pp. 1–88. Academic, New York.

GAMBELL, R., and MESSTORFF, J. 1964: Age determination in the whiting (*Merlangius merlangus* L.) by means of the otoliths. *J. Cons. perm. int. Explor. Mer 28*: 393–404.

GRAHAM, D. H. 1939: Breeding habits of the fishes of Otago Harbour and adjacent seas. *Trans. Proc. R. Soc. N.Z. 69*: 361–72.

GRAHAM, M. 1929: Studies of age-determination in fish. Part II. A survey of the literature. *Fishery Invest., Lond., Ser. 2, 11(3)*. 50 pp.

GUNTER, G. 1950: Correlation between temperature of water and size of marine fishes on the Atlantic and Gulf coasts of the United States. *Copeia 1950*: 298–304.

HAN, V. C. F. 1964: Jackass fish (*Nemadactylus macropterus*). *Rep. Div. Fish. Oceanogr. C.S.I.R.O. Aust. 1963–64*: 37–8.

HANABUCHI, N. 1967: Study on the nibe croaker, *Miichthys imbricatus* (*Matsubara*), in the East China and the Yellow Seas—(II). On the age and growth. *Bull. Seikai Reg. Fish. Res. Lab. 35*: 51–60.

HICKLING, C. F. 1930: The natural history of the hake. Part III. Seasonal changes in the condition of the hake. *Fishery Invest., Lond., Ser. 2, 12 (1)*. 78 pp.

——— 1933: The natural history of the hake. Part IV. Age-determination and the growth-rate. *Fishery Invest., Lond., Ser. 2, 13 (2)*. 120 pp.

HOAR, W. S. 1957: The gonads and reproduction. *In* Brown, M. E. (Ed.), "The Physiology of Fishes", Vol. 1, pp. 287–324. Academic, New York.

HODDER, V. M. 1965: The possible effects of temperature on the fecundity of Grand Bank haddock. *Spec. Publs int. Commn NW. Atlant. Fish. 6*: 515–22.

ILES, T. D. 1964: The duration of maturation stages in herring. *J. Cons. perm. int. Explor. Mer 29*: 166–88.

ILES, T. D., and JOHNSON, P. O. 1962: The correlation table analysis of a sprat (*Clupea sprattus* L.) year-class to separate two groups differing in growth characteristics. *J. Cons. perm. int. Explor. Mer 27*: 287–303.

IRIE, T. 1957: On the forming season of annual rings (opaque and translucent zones) in the otoliths of several marine teleosts. *J. Fac. Fish. Anim. Husb. Hiroshima Univ. 1*: 311–7.

——— 1960: The growth of the fish otolith. *J. Fac. Fish. Anim. Husb. Hiroshima Univ. 3*: 203–21.

JENSEN, A. C. 1965: A standard terminology and notation for otolith readers. *Res. Bull. int. Commn NW. Atlant. Fish. 2*: 5–7.

JUNE, F. C. 1970: Atresia and year-class abundance of northern pike, *Esox lucius*, in two Missouri River impoundments. *J. Fish. Res. Bd Can. 27*: 587–91.

KOHLER, A. C. 1964: 1963 ICNAF cod otolith exchange. *Res. Bull. int. Commn NW. Atlant. Fish. 1*: 22–7.

KOJIMA, K. 1967: Age and growth of the white croaker, *Argyrosomus argentatus* (Houttuyn), in the East China and the Yellow Seas. *Bull. Seikai Reg. Fish. Res. Lab. 35*: 61–76.

LACEPEDE, B. G. E. 1803: "Histoire Naturelle des Poissons", Vol. 5, p. 5. Plassan, Paris.

MCKENZIE, M. K. 1961: Fisheries research in the East Cape area. *Fish. tech. Rep. N.Z. mar. Dep. 3*. 9 pp.

MURAKAMI, S., and OKADA, K. 1967: Studies on the fishery biology of the sea bream, *Chrysophrys major* Temminck et Schlegel, in the East China and the Yellow Seas—III. Age and growth. *Bull. Seikai Reg. Fish. Res. Lab. 35*: 23–40.

NIKOLSKII, G. V. 1969: "Theory of Fish Population Dynamics as the Biological Background for Rational Exploitation and Management of Fishery Resources." English translation from Russian, edited by R. Jones. Oliver and Boyd, Edinburgh. 323 pp.

PARRISH, B. B., and SAVILLE, A. 1965: The biology of the north-east Atlantic herring populations. *Oceanogr. mar. Biol. 3*: 323–73.

PARRISH, B. B., and SHARMAN, D. P. 1958: Some remarks on methods used in herring "racial" investigations, with special reference to otolith studies. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer 143 (2)*: 66–80.

PHILLIPPS, W. J. 1926: Food of New Zealand fishes. *Trans. Proc. N.Z. Inst. 56*: 525–9.

PICKFORD, G. E., and ATZ, J. W. 1957: "The Physiology of the Pituitary Gland of Fishes." New York Zoological Society, New York. 613 pp.

RAITT, D. F. S. 1961: Some unusual otolith types on the Blϕden Ground in 1958 and their subsequent occurrence in the adult fisheries. *J. Cons. perm. int. Explor. Mer 26*: 329–35.

RASTOGI, R. K. 1966: A study of the follicular atresia and evacuated follicles in the Indian teleost, *Xenentodon cancila* (Ham.). *Acta biol. hung. 17*: 51–63.

RIBEIRO, A. de M. 1915: Fauna Brasiliense: Peixes V. Eleutherobranchios aspirophoros (Physoclisti): Chilodactidae. *Archos Mus. nac., Rio de J. 17*: 1–2.

RICHARDS, A. 1931: "Outline of Comparative Embryology." Wiley, New York. 444 pp.

RICHARDSON, J. 1839: Description of fishes collected at Port Arthur in Van Dieman's Land. *Proc. zool. Soc. Lond. 7*: 95–100.

ROUGHLEY, T. C. 1951: "Fish and Fisheries of Australia." Angus and Robertson, Sydney. 343 pp.

SCOTT, D. P. 1962: Effect of food quantity on fecundity of rainbow trout, *Salmo gairdneri*. *J. Fish. Res. Bd Can. 19*: 715–31.

SKERMAN, T. M. 1958: Seasonal variations in sea-water surface temperatures within New Zealand harbours. *N.Z. Jl Geol. Geophys. 1*: 197–218.

TONG, L. J., and ELDER, R. D. 1968: Distribution and abundance of demersal fish from trawl stations in the Bay of Plenty, New Zealand, 1961–63. *N.Z. Jl mar. Freshwat. Res. 2*: 49–66.

VOOREN, C. M. (in prep.): Observations on the postlarvae and juveniles of the New Zealand tarakihi, *Cheilodactylus macropterus* (Bloch and Schneider).

VOOREN, C. M., and TONG, L. J. (in press): A survey of the tarakihi, *Cheilodactylus macropterus* (Bloch and Schneider) in the East Cape area, New Zealand, 26–30 March 1971. *Fish. Res. Bull. (N.Z.) 9*.

WAITE, E. R. 1911: Scientific results of the New Zealand Government Trawling Expedition, 1907. Pisces, Part II. *Rec. Canterbury Mus. 1*: 157–272.

WALFORD, L. A. 1946: A new graphic method of describing the growth of animals. *Biol. Bull. mar. biol. Lab., Woods Hole, 90*: 141–7.

WAUGH, G. D. 1969: The work of the Fisheries Research Division of the Marine Department. *In* Slack, E. B. (Ed.), "Fisheries and New Zealand", pp. 75–94. Department of University Extension, Victoria University of Wellington.

WHEELER, J. F. G. 1924: The growth of the egg in the dab (*Pleuronectes limanda*). *Q. Jl microsc. Sci. 68*: 641–60.

WHITLEY, G. P. 1957: Ichthyological illustrations. *Proc. R. zool. Soc. N.S.W. 1955–56*: 56–71.

YAMAMOTO, K. 1956: Studies on the formation of fish eggs. I. Annual cycle in the development of ovarian eggs in the flounder, *Liopsetta obscura*. *J. Fac. Sci. Hokkaido Univ. Ser. 6, Zoology, 12*: 362–73.

YAMAMOTO, K., and YAMAZAKI, F. 1961: Rhythm of development in the oocyte of the gold-fish, *Carassius auratus*. *Bull. Fac. Fish. Hokkaido Univ. 12*: 93–110.

YAMAMOTO, K., and YOSHIOKA, H. 1964: Rhythm of development in the oocyte of the medaka, *Oryzias latipes*. *Bull. Fac. Fish. Hokkaido Univ. 15*: 5–19.

YAMAZAKI, F. 1965: Endocrinological studies on the reproduction of the female goldfish, *Carassius auratus* L., with special reference to the function of the pituitary gland. *Mem. Fac. Fish. Hokkaido Univ. 13*: 1–64.

INDEX

Age and growth, 28–34.
Age and length at first maturity, 41–42.
Age composition, 28, 29.
Age, determination, 13–27.
Age-frequency distributions, 37.
Age groups, 17, 19, 20, 21, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 38, 42.
Aldermen Islands, The, 14, 35, 43, 44.
Amsterdam Island, 11, 12, 35.
Annual growth, 29–33.
Annual record of marginal growth, 16, 17–19.
Antirostrum, 15.
Atresia, 49, 54.
Australian stocks of tarakihi, 44.
Australian waters, 12, 44, 45, 55.

Bay of Plenty, 11, 13, 17, 18, 20, 21, 23, 24, 25, 27, 28, 31, 32, 35, 36, 41, 43, 44, 45.
Brazil, 12.
Breeding biology, 35–45.
Breeding cycle, 35–37.

Calcification, 26, 27.
Cape Runaway, 40.
Chatham Islands, 11, 45.
Checks in zonation pattern, 16, 17, 26.
Cheilodactylidae, 11.
Cheilodactylus douglasii, 11.
Chilodactylus macropterus, 12.
Cichla macroptera, 11.
Clupea harengus, 27.
Clupea sprattus, 27.
Cod, 26.
Continental Shelf, 28, 35.
Conway Ridge, 14, 40, 42, 44.
Corpora atretica, 49, 50, 51, 54.

Dab, 54.
"Double rings", 26, 28.

East Cape, 14, 31, 32, 33, 40, 44.
East coast of New Zealand, 19, 44.
Eggs, mature, 49.
Eggs, resorbing, 49, 50.
Erythrocytes, 49, 50, 53.

Fecundity, 54, 55.
Female maturity stages, 36, 53.
Fin ray counts, 11.
Fish density, 29.
Flounder, 54.
Follicle cells, 46, 47.
Follicles, evacuated, 48, 49, 50, 53, 54, 55.
Follicular epithelium, 47, 48.
Ford-Walford regression, 32, 33.

Gadus morhua, 26.
Gametogenesis, 46–55.
Gastrulation, 46.
Germinal epithelium, 46, 47.
Golden Bay, 13, 14, 19, 22.
Goldfish, 54.
Gonad development, 24, 37.
Gonad growth, 26.
Gonadosomatic index, 34, 35, 39.
Gonads, annual weight changes in, 44.
Government trawling expedition 1907, 11.
Granulosa, 47, 48, 49, 50.
Great Australian Bight, 12.
Growth, 28–34.

Haddock, 54.
Hake, 16, 27.
Hawke Bay, 13, 14, 19, 20, 22.
Herring, 27, 37, 55.
Hyaline zone, 13–27.

Icelandic herring, 27.
Indian Ocean, 11, 12.

Juveniles, 15, 19, 21, 23, 26, 28.

Kaikoura Peninsula, 40.

Length-frequency distributions, 21, 22, 24, 36.
Length-weight relationships, 33-34.
Liopsetta obscura, 54.
Lottin Point, 14, 40, 41, 42, 44.

Male maturity stages, 36, 53.
Mar del Plata, 12.
Marginal increment, 15, 17-21, 23, 24, 25.
Material and methods, 13, 28, 35, 46.
Mature eggs, 49.
Maturity stage analysis, 37.
Maturity stage frequency, 40, 41, 42.
Maturity stages, 36, 38, 39.
Maturity stages, histological description of, 53.
Medaka, 54.
Mercury Bay, 14, 35, 44.
Merluccius merluccius, 16, 27.
Mitosis, 46, 51, 53.
Motiti Island, 13, 14, 16, 17, 25, 27, 28, 29, 30, 31, 35, 40, 41, 42, 43, 44, 46, 53, 54.

Nemadactylus macropterus, 11.
New South Wales waters, 11, 12, 44.
North Otago, 13, 14, 16, 19, 20, 22, 23, 24.
North Sea herring, 27.
North Sea sprat, 27.
Northern Hemisphere, 27.
Nucleoli, 47, 48.
Nucleus of otolith, 15, 20.

Oocytes, 46, 47, 48, 50, 51, 53, 54.
Oogenesis, 47–49, 50, 51.
Oogonia, 46, 47, 50, 51, 53.
Oolemma, 48, 49.
Opaque zone, 13–27.
Oryzias latipes, 54.
Otago waters, 11, 35.
Otolith readings, comparison of, 25–26.
Otolith zonation, analysis of, 16–20.
Otoliths, 13–27, 28, 35.
Ovaries, description of, 46.
Ovary, non-gametic components of, 49–50.

Petersen's method, 16, 19.
Plaice, 54.
Planktonic eggs, 55.
Plate Island, 13, 14, 25, 27, 28, 29, 30, 31, 35, 41, 43, 44, 46, 53.
Pleuronectes limanda, 54.
Porae, 11.
Primary oocyte, 47, 48, 53.

Ring counts and Petersen's method, comparison between, 19–20.
Ring groups, 17, 18, 19, 20, 21, 22, 23, 24.
Rostrum, 15.

Sagitta, 13.
St. Paul Island, 11, 12, 35, 45.
Salmo gairdneri, 54.
Sampling dates, 28.
Sampling techniques, 13.
Seasonal growth, 28.

Sex ratio, 43–44, 45.
Sexual dimorphism, 11.
Slipper Island, 13, 14, 25, 28, 29, 30, 31.
Somatic growth, 26.
South Island, 28.
Southern New Zealand waters, 44.
Spawning period, 19, 38, 40, 41, 42, 43, 44, 45, 54, 55.
Spermatids, 46, 52.
Spermatocytes, 52.
Spermatogenesis, 46, 51–52, 53.
Spermatogonia, 51, 52, 53.
Spermatozoa, 46, 52.
Spermiation, 52, 53.
Stewart Island, 11.
Tasman Bay, 13, 14, 19, 21, 22.
Tasmania, 11, 12.
Teleost labyrinth, 13.
Testes, description of, 46.
The Aldermen Islands, 14, 35, 43, 44.
Three Kings Islands, 11.
Vacuolated oocytes, 53.
Vacuolation, 48.
Victoria, 12.
Vitellogenesis, 48–49.
von Bertalanffy growth equation, 32.
Western Australia, southern, 12.
Whiting, 44.
Yellow body, 50, 51.
Zona radiata, 48, 49.
Zonation pattern, 16, 17, 27.
Zone counts, 16.
Zone formation and age, 24.
Zone formation in different sea areas, 24–25.
Zones, otolith, 13–27.

Bulletins of the Fisheries Research Division

No.

1. The New Zealand Cetacea. By D. E. Gaskin. Published in 1968. 92 pp.

2. *Galaxias maculatus* (Jenyns), the New Zealand whitebait. By R. M. McDowall. Published in 1968. 84 pp.

3. Phytoplankton productivity in Tomahawk Lagoon, Lake Waipori, and Lake Mahinerangi. By S. F. Mitchell. Published in 1971. 87 pp.

4. Some aspects of the bionomics of fish in a brown trout nursery stream. By C. L. Hopkins. Published in 1970. 38 pp.

5. Reproduction, early life history, and age-growth relationships of the New Zealand pilchard, *Sardinops neopilchardus* (Steindachner). By Alan N. Baker. Published in 1972. 64 pp.

6. The biology of the New Zealand tarakihi, *Cheilodactylus macropterus* (Bloch and Schneider). By L. J. Tong and C. M. Vooren. Published in 1972. 60 pp.

7. An analysis of the statistics on the fishery for tarakihi, *Cheilodactylus macropterus* (Bloch and Schneider), in New Zealand waters from 1936 to 1969, with notes on the trawl fishery in general. By C. M. Vooren (in press).

8. Lakes Rotorua and Rotoiti, North Island, New Zealand: Their trophic status and studies for a nutrient budget. By G. R. Fish (in press).

9. A survey of the tarakihi, *Cheilodactylus macropterus* (Bloch and Schneider), in the East Cape area, New Zealand, 26–30 March 1971. By C. M. Vooren and L. J. Tong (in press).

10. The relation between primary productivity, nutrients, and the trout environment in some New Zealand lakes. By A. M. R. Burnet and Denise A. Wallace (in press).

Printed by "The Evening Post", Wellington, by authority
A. R. Shearer, Government Printer.